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By JOHN A. KING

ANN ARBOR
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INTRODUCTION

THE active participation of animals in their intraspecific relations is a basic factor in the evolution of the species. Since most intraspecific relations are social, the course of evolution of a species may be determined through the effect of social behavior on population size, migration rate, assortative mating, inbreeding, and selection pressure. The density and distribution of a species throughout its range often varies with its social behavior. Highly social species congregate in dense local populations, leaving other parts of a homogeneous habitat unsettled. In contrast, solitary species may occur only thinly distributed throughout their range. Migration rate may be influenced by the search for mates or by the expulsion of some individuals from particular homesites. Almost any departure from panmictic breeding results in assortative mating, which may depend upon the distribution of individuals, upon their migration, or more directly upon their selection of mates. Offspring which are not forced away from their natal home by other individuals may remain to mate with their siblings or parents and thereby increase the amount of inbreeding. The pressure of selection on a species is often reduced by the co-operative activities of its individuals in sheltering one another, in guarding against enemies, and in securing food. It is largely through social relationships that a species may take an active part in determining the rate and direction of its evolution.

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*A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

One seemingly paradoxical effect which the behavior of a highly social species has upon its population is that dense local populations, arising from the mutual benefit afforded the individuals, may lead to detrimental overcrowding. Those social relations which benefit the species to such an extent that mortality is reduced and density increases may ultimately bring about a severe decline in the population. The adaptive value of a social behavior which first causes a population increase and then a population decline may be questioned if there is not some regulatory mechanism to prevent such a decline. Elton (1942) has suggested that social species not only derive benefit from their social habits, but also control their population density by a social regulatory mechanism. Consequently, the social activities of a species may tend to keep the population density at an optimum.

The modifiability of social behavior depends on (1) the genetic changes in the population and/or (2) the ability to learn new social habits and to pass them on from one generation to the next. The same processes which influence organic evolution are also at work in changing those behavioral traits which are determined by the germ plasm. Inasmuch as evolutionary processes are governed by social behavior, those social traits which are inherited may experience a particularly accelerated rate of evolution. Most behavior, however, is so influenced by the environment that certain behavioral traits may be learned. Although learned behavior cannot be completely assayed, it is necessary to consider the extent of its effect on all behavior because learning is much more plastic to changes in the environment than is germ plasm. This plasticity of learned behavior to a certain extent releases animals with the capacity to learn from slow genic changes, and consequently their accumulation of learned behavior throughout succeeding generations may be exceptionally rapid. The limits of social evolution may soon be reached, however, as a result of retarded organic changes.

The objectives of this study are (1) to describe the social behavior of a social rodent, the prairiedog, (2) to measure the effect its societies have on the environment, (3) to assess the relation between social behavior and population dynamics, and (4) to discover social mechanisms which may regulate population density.

The black-tailed prairiedog (Cynomys ludovicianus) was selected for this study because of the numerous and varied social relations within its densely populated towns, where individuals presumably derive certain advantages from group life. In addition, its diurnal, sedentary habits and open grassland habitat facilitate the observation of its social behavior in the native environment.

Acknowledgments

This study was made under the direction of Professor Lee R. Dice, to whom I wish to express my appreciation. Dr. Francis C. Evans provided many stimulating suggestions both in the field and at the Laboratory of Vertebrate Biology. The National Park Service, through the recommendation of Victor H. Cahalane, chief biologist, provided facilities for the study of prairiedogs in Wind Cave National Park. James Cole, regional biologist, assisted in mapping the burrows and also provided useful reports on the prairiedogs of the park. William Watson, chief ranger, assisted with some of the measurements and identifications of the vegetation on the prairiedog town. Mrs. Rita Cohen carefully reviewed the manuscript for grammatical errors. My wife, Joan M. King, assisted me in the field work and in preparing the report. Funds made available through the Veterans Readjustment Act and the R. B. Jackson Memorial Laboratory contributed to the expenses incurred in making the study and in preparing the report. Publication was made possible by a grant from the Horace H. Rackham School of Graduate Studies.

Area Studied

The study was conducted in the southeastern edge of the Black Hills, Custer County, South Dakota. All observations on prairiedogs here reported were made within the boundaries of Wind Cave National Park. The park contains seven separate prairiedog towns, all of which were seen and three of which were cursorily examined. The most detailed study was made in Shirttail Canyon, where a large prairiedog town is situated one and one-half miles from the southern border of the park, in sec. 10, T. 6 S., R. 5 E.

The advantages of the location within a national park include the availability of reports and maps prepared by the park service, the protection of the prairiedogs from human destruction, and the preservation of the large herbivores characteristic of the region.

Duration of Study

Approximately 40 weeks were employed in collecting data for this study. The periods of time spent in the field are as follows: in 1948, from July 7 to August 20; in 1949, from July 5 to August 27; in 1950, from February 17 to August 31; in 1952, from May 11 to May 21.

METHODS

The methods employed in this study include live trapping, marking, and observing the prairiedogs. The area occupied by the town was marked off in grid fashion to facilitate observation of position and movements of the animals. The quantity of the vegetation on the town was ascertained by belt and line transects and by the clipped quadrat method.

Traps. — Since most kinds of box traps proved unsatisfactory, it was necessary to construct a trap which corrected some of their defects. A box trap of an original design used in 1950 was more successful in attracting shy prairiedogs, retaining the captured individuals, withstanding strong winds, and permitting the capture of more than one individual at a time.

In order to capture the most wary individuals, a trap corral made of chicken-wire screen with one-inch mesh was employed. Prairiedogs were attracted into the corral with oats, whereupon the observer pulled a cord which caused a door to drop.

There was usually a lapse of three days between the time the traps were set and the capture of the first prairiedog. The time was longer or shorter depending on the amount of natural food available.

There were no cases of trap mortality. A few pups that accidentally spent the night in traps were in a comatose state the next morning, but all rapidly recovered. Animals left in the traps for a long time during the heat of the day frothed at the mouth and appeared to be exhausted. Most individuals were released shortly after they were captured. The average time spent in a trap at any one time by a prairiedog is estimated to have been approximately three hours.

The traps were set near active burrows. No grid or other schematic pattern was used. Usually, only a small segment of the town was trapped at any one time, so that traps could be placed in concentrations of one or more to a burrow. The prairiedogs avoided any conspicuous strange objects near their burrows and did not approach the traps close enough to be drawn by the bait unless the traps were so concentrated that an animal could not move about its home range without coming into contact with the bait.

Marking and recording. — When a prairiedog was captured, it was examined to ascertain its sex, it was weighed to the nearest ounce, its toes were clipped, and its fur was marked with dye. The toe clipping made the identification of the animals possible between molts and from year to year. Nyanzol A, a black fur dye manufactured by the Nyanza Color and Chemical Company[1], was applied with a brush in various patterns on the sides, head, and back of the prairiedog in order to make it readily identifiable in the field. No two patterns of marks were exactly alike; those somewhat similar were generally used on animals dwelling far apart. The dye remains on the summer pelage until the fall molt — about 3 months. It fades somewhat on the winter pelage because the animals retain this pelage for a longer period of time. Molting, of course, necessitated the recapture and redyeing of the prairiedogs.

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[1] 109-111 Worth Street, New York 13, N. Y.

The animals appeared to be little affected by toe clipping beyond the initial disturbance. Toes were numbered in such a way that it was necessary to cut no more than one toe from each foot. The removal of the distal phalanx often caused heavy bleeding, particularly in an overheated animal.

The dye seemed to have no effect upon the behavior of the prairiedogs toward one another. Even those individuals which were marked conspicuously or which were almost completely dyed were treated by the other animals in the same manner as unmarked individuals of similar age and sex. There was no evidence that the dye made them more vulnerable to attack from predators.

Observations. — Most observations were made from an elevated blind on a rise of ground at one edge of the study area, a position enabling identification of any prairiedog in the area. Some prairiedogs, however, could not be seen when they entered tall grass at the far edge of the study area. When some individuals moved into this region in the summer of 1950, a smaller blind was constructed beyond the western edge of the town.

Notes on behavior and movement of the prairiedogs were taken in chronological order, and the time of each event was recorded. The position and number of each prairiedog were ascertained by using both a map of the study area, showing the position of each burrow, and the record sheets of the marked prairiedogs. Occasionally, tables of the contacts between animals and maps of their movements were made.

Most observations were made with 8-power binoculars. A 20-power telescope mounted on a tripod was used for identifying and observing prairiedogs farther away from the blind and also for observing food preferences of the animals at close range. Photographic equipment was usually brought to the blind each day for recording behavior of special interest.

Mapping. — A map of the study area was made for each of the successive years of study, showing the position of each burrow and its stage of development. Mapping was done by subdividing the area into quadrats 50 feet square, with the sides corresponding to the cardinal points of the compass. Each corner of a quadrat was marked with a tall, visible stake so that each quadrat could be identified from a distance. The positions of the burrows in a quadrat were ascertained by measurements with a steel tape. These positions were checked with an alidade by Mr. Cole, regional naturalist, in 1950. Aerial photographs were also made in 1950 after the burrows had been marked by circles of mason's lime one foot in diameter. The final map, which included the most recent additions to the study area, was checked with each burrow on August 25, 1950.

A total of 614 burrows was mapped on the study area. Each burrow was classified according to the size of the crater and signs of activity and was assigned to one of the following 3 categories: (1) large, well-formed crater, much used; (2) small crater or mound, frequently used; (3) no crater or mound, seldom used. The concentric circles in Figure 4 indicate the position of each burrow and its classification.

DESCRIPTION OF THE AREA

The topography of the region is a gently rolling limestone plateau with an elevation of nearly 1,000 feet above the plains to the east. The elevation above sea level varies from 4,000 to about 4,700 feet on a few hilltops. The relief is sharp only where canyons, such as Shirttail, Coldbrook, and Beaver Creek, dissect the plateau. Pink and gray limestone rocks are exposed where the intermittent streams have cut into the canyon sides. The soils are immature, strewn with rocks and pebbles or consisting mostly of light reddish clay.

Shirttail Canyon, where this study was made, is situated in the southwestern corner of Wind Cave National Park. The temporary stream in the canyon is dry for most of the year, except for small, isolated, spring-fed holes. During heavy cloudbursts it may become quite swollen; a rise of 12 feet was reported in 1947. Most of the terrace and floor of Shirttail Canyon are bordered by steep slopes. The terrace occurs as small benches on both sides of the canyon 30 to 50 feet above the canyon bottom. Dense stands of pine (Pinus ponderosa) occur on the canyon slopes and on north-facing slopes of steeper hills. A few elms (Ulmus), hackberries (Celtis), and box elder (Negundo) are scattered along the dry stream bed. The floor and terrace are covered with mixed grasses (Bromus, Agropyron, Bouteloua) and a variety of forbs. (See list of species under section on Food.)

The soils of Shirttail Canyon are for the most part sedimentary, with an irregular distribution of deposits and a stratified profile. In some places the upper stratum is enriched by humus from the grasses and forms a thin topsoil four to six inches deep. In other places, where erosion has been greater, especially on the slopes, heavy gravel or rocks are exposed. Prairiedog burrows only a few feet apart may exhibit sand, gravel, or clay in the craters. At a single burrow several horizons through which the tunnel has been dug are often evident in the composition of the excavated earth.

The climate in this region is typically continental, with great daily and seasonal fluctuations in temperature. The sun, shining through clear skies, frequently raises the temperature well above freezing in midwinter, wheras summer temperatures occasionally rise above 100° F. The mean annual temperature recorded at Hot Springs, South Dakota, is 47°, with a mean monthly temperature of 10.6° in the coldest month (January) and 87.4° in the warmest month (July). The average length of the growing season is 138 days (Johnson, 1933). In Rapid City, South Dakota, 18 days of the year, on the average, have temperatures of 90° or above, and 157 days have temperatures of 32° or below; the percentage of sunshine is 64 (Blair, 1942).

Most of the precipitation in this region falls during the spring, from April to June, with May being the wettest month (3.04 inches) and February the driest month (0.47 inch). The average annual precipitation is 18.67 inches at Hot Springs (Johnson, 1933). Precipitation in the early spring months is frequently in the form of snow, which seldom stays on the ground for a long period because of the generally warm air temperatures. Local thundershowers during the summer are common. Heavy fogs and mists are often characteristic of the early spring wet season.

The Shirttail Canyon prairiedog town occupies an area of approximately 75 acres covering part of the canyon floor and extending over some of the terrace on both sides. Here the canyon has been widened by a U-shaped bend of the stream (Pl. I). The large segment of the terrace which is inside the bend of the canyon is wider than the parts which are outside and is shaped like a peninsula, separated from the canyon floor by steep slopes on both sides. It joins the canyon floor at one end by a gentle incline. At the other end forested hills cut it off from the surrounding terrain. The area of the terrace inside the bend is a little more than 80 acres. Part (11.7 acres) of this prairiedog town in situated on the end of the terrace which is connected with the canyon floor by a gentle incline.

That part of the Shirttail Canyon town situated on the highest section of the terrace inside the bend of the stream was studied in detail. This area is designated as Ward A or the "study area" (Pl. I). A few observations were made on the lower section of the terrace, adjacent to the canyon floor, designated as Ward B. These two wards were separated by a gentle rise of 15-20 feet in the level of the terrain and by a few scattered pine trees. In 1948 the area occupied by the prairiedogs on Ward A covered approximately 5.2 acres.

The sides of the canyon above the terrace are steep slopes and limestone-faced cliffs. Many of the slopes are forested with pine trees. On the inside of the bend the terrace is connected with the present floor of the canyon by a gradual incline. Elsewhere it is separated from the floor by steep slopes. Above the site of the prairiedog town the canyon floor is constricted by a wall of rocks which seals off the upper part of the canyon except for the stream channel. Below the town the floor remains wide for almost a mile before it is pinched off by the canyon sides. The terrain above the canyon is rolling, with a substratum predominantly of gravel.

The prairiedogs which inhabit this town are more or less restricted to the floor and terrace of the canyon because of the steepness of the walls. Expansion of the colony is possible only along the floor below the present site and over the terrace inside the bend.

LIFE HISTORY

Published accounts of prairiedogs have dealt with many phases of their life history. Their food habits have been studied by Kelso (1939) and by Merriam (1901), their burrows by Merriam (1901) and by Scheffer (1937), their growth by Johnson (1927), their reproduction by Anthony and Foreman (1951), and their ecologic responses by Scheffer (1947) and by Osborn and Allan (1949). More general accounts have been given by Bailey (1926, 1931) and by Seton (1929). Other general notes concerning their life history have been reported from time to time, particularly in the Journal of Mammalogy. Some information has been collected on other species of Cynomys, primarily by Longhurst (1944) on C. gunnisoni and by Stockard (1929, 1930) on C. leucurus. The life history summary presented in this study is intended to aid in the interpretation of the population dynamics and social structure of these animals.

Food Relations

The vegetation in this prairiedog town was much modified by the feeding of the animals, by their burrows, and by their clipping of the tall vegetation. These activities completely denuded some areas of all vegetation, particularly around the burrows. In the center of their areas of activity forbs had replaced the original grass cover. Around the periphery of the town much of the original vegetation remained. The natural vegetation varied somewhat from place to place in the study area because of the heterogeneity of edaphic features.

Kinds of vegetation available. — The principal herbaceous species found on Wards A and B in Shirttail Canyon are listed below;[2] those species eaten by prairiedogs (as ascertained by observation only) are marked with an asterisk:

Poaceae: wire grass (Aristida longiseta)*, spear grass (Stipa viridula), Texas crab grass (Schedonnardus paniculatus), blue grama grass (Bouteloua gracilis)*, tall grama grass (Bouteloua curtipendula), buffalo grass (Buchloë dactyloides), brome grass (Bromus japonicus)*, wheat grass (Agropyron smithii), witch grass (Panicum sp.), big bluestem (Andropogon scoparius). Cyperaceae: sedge (carex filifolia). Iridaceae: iris (Sisyrinchium angustifolium). Polygonaceae: knotweed (Polygonum ramosissimum)*, knotweed (Polygonum buxiforme). Chenopodiaceae: goosefoot (Chenopodium album). Amaranthaceae: pigweed (Amaranthus retroflexus)*. Nyctaginaceae: umbrella wort (Allionia linearis). Portulacaceae: whitlow wort (Paronychia sp.). Brassicaceae: wall flower (Cheirinia inconspicua). Grossulariaceae: cinquefoil

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[2] Identifications were kindly made by William Watson, chief ranger, Wind Cave National Park. The names used are those of Rydberg (1932) or in a few instances McIntosh (1931).

(Potentilla sp.). Fabaceae: white sweet clover (Melilotus officinalis), few-flowered psoralea (Psoralidium tinuiflorum), silvery psoralea (Psoralidium argophylum), locoweed (Geoprumnon plattense), prairie clover (Petalostemon purpureus), locoweed (Oxytropis plattensis). Oxalidaceae: yellow sorrel (Xanthoxalis corniculata)*. Simarubaceae: milkwort (Polygala alba). Euphorbiaceae: spurge (Chamaesyce sp.)*. Malvaceae: scarlet mallow (Sphaeralcea coccinea)*. Cactaceae: cactus (Neomamillaria sp.). Onagraceae: evening primrose (Onagra albicaulis), evening primrose (Meriolix serrulata), butterfly weed (Gaura sp.). Asclepiadaceae: milkweed (Asclepias pumila). Boraginaceae: stickweed (Lappula sp.), stickweed (Lappula occidentalis)*, puccoon (Lithospermum gmelini), (Lithospermum linearifolium), (Onosmodium occidentale). Verbenaceae: vervain (Verbena bracteosa), vervain (Verbena hastata). Lamiaceae: savory (Clinoposium sp.). Solanaceae: nightshade (Solanum nigrum)*. Scrophulariaceae: mullein (Verbascum thapsus)*, beardtongue (Pentstemon sp.). Plantaginaceae: plantain (Plantago purshii). Compositae: blazing star (Liatris punctata), brownweed (Gutierrezia sarothrae), golden aster (Chrysopsis villosa), goldenrod (Solidago pallida), goldenrod (Solidago sp.), fleabane (Erigeron flagellaris), mare's tail (Leptilon canadense), black-eyed susan (Rudbeckia hirta), cone flower (Ratibida columnifera), sage (Artemisia gnaphalodes), sage (Artemisia frigida), thistle (Cirsium sp.)*, fetid marigold (Boebera papposa)*. Cichoriaceae: skeleton weed (Lygodesmia juncea)*.

Species of plants other than those indicated above are eaten by prairiedogs. Kelso's study (1939) of 247 stomachs of prairiedogs, 228 of which were taken from four localities in Montana, shows that the preferred item of food is grass, which totaled 51.5 per cent of the volume in the stomachs analyzed. The amount of grass consumed by prairiedogs in the Shirttail Canyon town probably is not so high as the percentage quoted by Kelso indicates, since the prairiedogs seem to rely mostly on forbs for food, owing to the paucity of grass in some parts of the town.

A variety of forbs thrive on the area, most of them providing food for the animals. Certain plants on the study area, Artemisia for example, although probably not eaten by the prairiedogs, fail to dominate the other vegetation because the animals keep them clipped to within a few inches of the ground.

The parts of the plants selected for food are largely those of high energy or high water content. Usually, the succulent, meristematic tissue at the base of the grass blades or the seeds and fruits of forbs are eaten first. Considerable quantities of crude fiber and cellulose are also ingested and appear to be selected at times. More often the fibrous parts are taken along incidentally with the parts containing more nutritious food. Thistles (Cirsium), eaten in abundance during the drier part of the season, were selected perhaps for their high water content.

Quantities of vegetation available. — Types of vegetative cover, in

TABLE I

Percentage of soil and plant coverage by principal vegetation in successive 50-foot sections of a line transect across Wards A and B. Bare soil decreases toward outer edge of Ward A.

	Ward B					Ward A			
	0-50	50-100	100-150	150-200	200-250	250-300	300-350	350-400	400-450
Bare soil and rock	60	50	51	70	86	54	51	20	08
Grasses									
Aristida	02	..	..	..	..	..	..	..	..
Schedonnardus	12	02	..	02	..	..	12	29	03
Bouteloua	09	23	..		..	10	06	03	..
Agropyron	..	..	..	..	..	04	03	..	..
Andropogon	..	..	..	..	03	..	..	..	..
Mixed Bouteloua, Schedonnardus and Agropyron	..	..	..	..	..	..	..	22	..
Mixed Agropyron and Schedonnardus	..	..	..	..	..	..	..	05	..
Mixed Bromus and Bouteloua (short)	..	..	..	..	..	..	..	..	47
Mixed Bromus and Bouteloua (tall)	..	..	..	..	..	..	..	..	34
Carex	02	..	..	..	..	..	..	..	..
Forbs									
Polygonum	..	..	03	..	..	..	..	..	..
Xanthoxalis	..	06	08	..	..	..	04	..	..
Verbena	..	03	10	..	..	..	..	03	..
Erigeron	..	..	..	09	..	..	..	..	..
Leptilon	15	10	16	03	..	14	10	11	03
Artemisia	..	..	..	03	03	10	03	..	..
Cirsium	..	..	..	..	05	..	04	..	..
Other plants	..	06	12	13	03	08	07	07	05
Total per cent	100	100	100	100	100	100	100	100	100

1948, were measured along a 450-foot line transect oriented north and south approximately through the middle of Wards A and B. The amount of ground covered along the transect by each genus of plant was measured to the nearest inch, and its percentage of cover was calculated for every section of 50 feet.

The data from the line transect show a difference in percentage of bare earth between Wards A and B and also a downward gradation in percentage of bare earth toward the outer edge of Ward A (Table I). Ward B has a higher percentage of bare earth in most of the 50-foot sections than does Ward A. The two 50-foot sections of Ward A (350-400 ft., 400-450 ft.) at the outer edge of the prairiedog town contain the highest percentages of grass cover. Forbs predominate in Ward B and in the 50-foot sections of Ward A (250-300 ft., 300-350 ft.) adjacent to Ward B.

The air-dry weights of vegetation taken from 20 randomized clipped quadrats (Table II) further illustrate the difference in the relative abundance of grasses and forbs between Wards A and B. Over ten times as much grass by weight is present in Ward A, at the edge of the town, as in Ward B, near the middle. In contrast, the quadrats in Ward B have a greater weight of forbs than those in Ward A. The total weight of the vegetation per quadrat is over twice as great in Ward A as in Ward B. Ward B, situated closer to the middle of the town, was occupied by prairiedogs before 1938, whereas Ward A, at the edge of the town adjacent to a large grass field, became inhabited by prairiedogs after 1938.

Table II

Air-dry weight in grams of clipped vegetation on random square-yard quadrats. Weight of vegetation differs in the two wards. Ward A is at the edge of the Shirttail Canyon town.

Quadrat	Weight of Grasses, Grams	Weight of Forbs Grams	Total Weight, Grams
Ward A			
Ji	89.8	6.5	96.3
Ik	20.0	0	20.0
Ii	111.0	0	111.0
Oh	24.0	0	24.0
Jl	18.0	0.5	18.5
Pg	22.3	7.0	29.3
Qj	4.5	4.7	9.2
Ml	17.7	22.5	40.2
Jh	140.7	9.0	149.7
Hg	61.0	0	61.0
Totals	509.0	50.2	559.2
Ward B			
Qp	5.5	10.5	16.0
Op	16.5	13.0	29.5
Np	11.5	18.0	29.5
Pp	1.0	72.5	73.5
Pn	2.5	18.5	21.0
Mn	13.5	5.0	18.5
Jp	0	5.0	5.0
Ho	0	21.0	21.0
Hn	0	7.0	7.0
In	0	7.5	7.5
Totals	50.5	178.0	228.5

Frequency indices from a series of uniformly spaced square-foot quadrats along two belt transects placed at right angles to each other across the middle of Ward A show a rough zonation of the vegetation. The presence or absence of a species of plant was recorded for each quadrat at ten-foot intervals along the transects. In all, 86 quadrats were examined. The data, presented in Tables III and IV and in Figure 1, demonstrate a rough zonation of vegetation in which forbs predominate in those zones of Ward A which are proximal to Ward B and diminish in abundance in the outer zones where grasses predominate. This arrangement of the vegetation in zones is somewhat similar to that in the zones found by Osborn and Allan (1949) in an abandoned prairiedog town in Oklahoma. Since Ward A represents only a section of a prairiedog town, it does not contain the complete concentric zones of an entire town, such as that described by Osborn and Allan.

Effects of feeding upon vegetation. — The distribution of kinds and quantities of plants in a prairiedog town is due to the feeding of the prairiedogs. Intensive utilization of the original grass cover by the prairiedogs results in a depletion of the grass in the middle of the town. Forbs replace most of the grass and provide food for the inhabitants. Some grass persists, however, in the middle of a town after prairiedogs have inhabited it for a long period.

Grasses cannot withstand the feeding of the prairiedogs as well as can the forbs. Consequently, forbs flourish in the new habitat created for them through the destruction of the grass. Probably no species can resist constant destruction by feeding. As a result, the species of forbs preferred by the prairiedogs decrease in abundance, and less preferred species increase. Domination of the vegetation by a less preferred species is probably restricted by the feeding habits of the prairiedogs. First, their food habits are modified with changes in the vegetation; the more abundant a less preferred species becomes, the more it is used for food. Thus, the area is opened for reinvasion by other species. Second, the feeding range of each individual usually contains several different vegetation types (Fig. 1). A prairiedog may for a time feed primarily on one type of vegetation and neglect a less preferred type, which may be replaced in the following year by the preferred species. For example, the prairiedogs fed about the edges of Ward B at a time when part of the ward had become almost entirely covered by edible trailing fleabane (Erigeron flagellaris). In the following year competing species of plants partly replaced the fleabane. The new plant species provided food for the prairiedogs, and they again fed in the middle of the area. These shifts in the feeding range and the resulting changes in vegetation are analogous to the human practice of fallow farming.

Another analogy to human farming methods is offered by the cultivation of the soil by the burrowing of the prairiedogs. Subsoil is thrown out on the surface of the ground and is exposed to invasion by forbs, which, on the topsoil, cannot compete with the grasses. The earth exposed about the burrows frequently is covered by plants not found abundantly elsewhere in the region. Fetid marigold (Boebera papposa), scarlet mallow

TABLE III

Presence or absence of certain species of plants along a belt transect, on quadrats one foot square, taken every tenth foot. Transect oriented north and south through the middle of the Shirttail Canyon prairiedog town, Ward A. Roman numerals indicate possible vegetational zones.

	South III						II										I												IV North												
	400		380		360		340		320		300		280		260		240		220		200		180		160		140		120		100		80		60		40		20		0
Grass and Sedge																																									
Bouteloua	X	X	X	X	X	X	X	X	X	X	X					X											X									X			X	X	X
Agropyron			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X															X	X		X		X	
Bromus	X	X	X	X	X	X	X	X	X	X	X	X																													
Buchloe	X							X	X		X	X	X	X	X	X						X						X					X					X			
Aristida																															X	X	X				X				X
Carex			X																															X		X		X		X	
Forbs																																									
Asclepias																														X	X	X		X							
Boebera													X							X							X		X	X	X		X		X		X	X	X		
Paronychia																																	X				X	X	X	X	X
Cirsium																																			X	X			X	X	
Psoralidium	X	X						X	X			X					X	X		X									X												
Erigeron										X		X		X				X	X																		X				X
Chamaesyce															X			X	X	X								X	X						X						
Xanthoxalis																	X			X								X							X						
Lappula sp.															X							X	X		X	X															
Polygonum															X							X	X		X	X															
Lappula occid.																	X				X	X	X		X	X	X	X	X		X	X	X	X	X		X	X	X	X	
Clinoposium							X	X			X	X	X	X	X	X	X		X	X				X		X	X	X	X	X	X	X	X		X				X		X

TABLE IV

Presence or absence of certain species of plants along a belt transect, on quadrats one foot square, taken every tenth foot. Transect oriented east and west through the middle of the Shirttail Canyon prairiedog town, Ward A. Roman numerals indicate possible vegetational zones.

	West III													II						I																			IV East								
	0		20		40		60		80		100		120		140		160		180		200		220		240		260		280		300		320		340		360		380		400		420		440		460
Grass and Sedge																																															
Bromus	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X																													X	
Agropyron	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X				X							X						X					
Bouteloua	X	X	X	X		X	X		X	X	X	X	X	X		X			X			X	X	X		X	X											X		X	X		X	X	X		X
Carex	X	X	X												X									X														X		X	X	X	X	X	X	X	X
Aristida																																										X		X	X	X	X
Schedon											X	X	X	X	X	X	X	X		X	X	X	X		X				X			X	X			X		X	X	X				X	X		
Forbs																																															
Lygodesmia						X	X								X	X	X																										X	X	X		X
Paronychia																											X															X	X		X		X
Solanum																							X			X			X						X		X				X						
Artemisia			X			X						X																															X	X	X		X
Plantago														X	X	X								X		X													X			X		X			
Erigeron																X	X	X	X	X	X	X		X	X				X	X									X		X	X					
Verbena														X			X	X		X	X			X		X				X	X	X	X	X	X	X	X	X	X								
Clinoposium													X		X	X	X	X	X	X	X		X	X	X		X	X			X	X		X							X				X		
Lappula occid.													X		X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X									
Lappula sp.														X							X		X	X				X	X	X		X			X												
Boebera																	X											X						X				X			X						

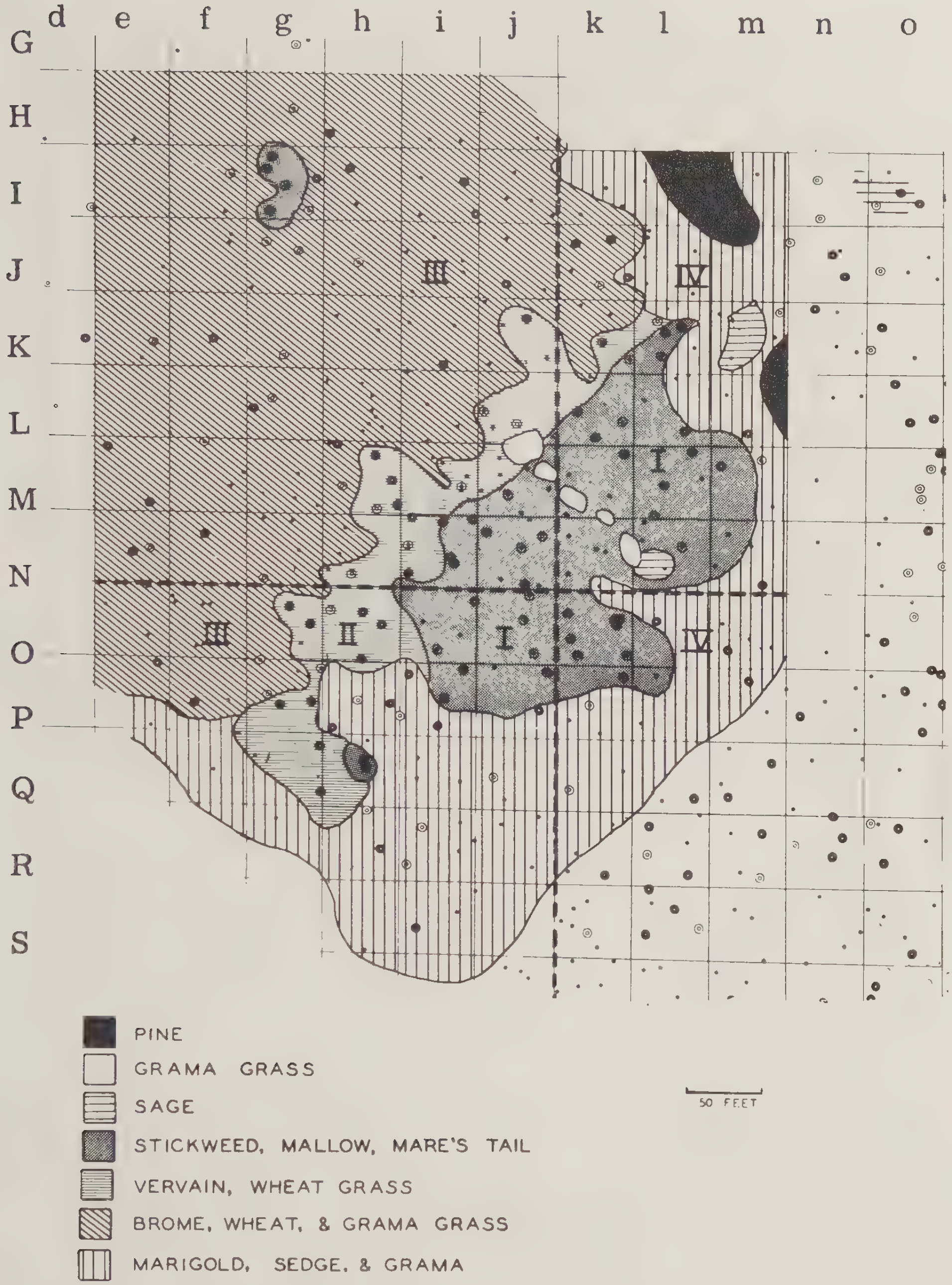

Fig. 1. Map of vegetation on Ward A of the Shirttail Canyon town in 1950. Vertical lines are oriented east-west; horizontal lines, north-south. Heavy dashed lines indicate position of belt transects. Roman numerals indicate possible vegetative zones (See Tables III and IV).

(Sphaeralcea coccinea), black nightshade (Solanum nigrum), and pigweed (Amaranthus retroflexus), for example, are species which occur almost exclusively on the subsoils exposed about a prairiedog burrow. These plants, which have been more or less "cultivated" by the prairiedogs, are often eaten and at times appear to be important food items.

Feeding behavior. — Prairiedogs spend most of the day eating and foraging for food. The mean proportional time spent in feeding by 11 animals watched individually for the greater part of 11 days, or a total of 82 hours, was 57 per cent of their active day (Table V). Other activities of the day included the making of social contacts (6 per cent), moving about (6 per cent), staying in burrows (15 per cent), acting alert (13 per cent), and miscellaneous activities (3 per cent). Since all of the prairiedogs could not be watched on the same day, the percentages are not directly comparable. In general, young animals spent a larger proportion of their active day feeding than did mature animals. Frequently, the behavior of the prairiedogs was affected by a particular activity or circumstance which reduced the amount of time spent in feeding. On days when the temperatures were over 100° F. or when the animals were severely frightened, they spent less time feeding and more of the day in burrows. An adult male was building a new nest on the day he was observed and therefore spent much of his time digging and carrying nesting material into the burrow. Strong winds often kept the prairiedogs more alert and cautious than they were on calm days. On the day ♂ 37 was observed, he was alert in guarding his range from a strange individual. Despite these other factors which interrupt the amount of time spent in feeding, it still represents the major part of activity.

Table V

Percentage of time spent in various activities by 11 prairiedogs observed individually for an entire day. A total of 82 hours of observation during July and August of 1948 and 1950 on Ward A of the Shirttail Canyon town.

Number of Animal	Sex	Age	Total Minutes	Feeding	Inside Burrow	Alert or Standing	Social Contacts	Moving About	Miscellaneous
6	♂	Ad.	436	50	18	8	5	10	9
10	♂	Ad.	761	74	6	11	5	5	0
16	♀	Ad.	338	43	25	14	9	5	3
17	♀	Ad.	421	62	17	8	4	3	5
24	♂	Ad.	341	57	25	6	5	4	3
37	♂	Ad.	576	33	8	42	5	12	0
51	♀	Ad.	559	48	11	30	5	4	3
88	♀	Im.	313	64	24	4	5	4	0
89	♂	Im.	401	71	17	4	4	3	1
90	♀	Im.	388	73	3	5	11	8	0
130	♂	Im.	369	57	14	15	8	5	2
Mean percentage				57	15	13	6	6	3

Prairiedogs find their food by smelling along the ground until a morsel is discovered. Each kind of food is collected and consumed in a characteristic fashion. Large leaves and fruits are bitten off at the base and eaten while the animal sits up and holds them in its forepaws. A prairiedog procures grass by pulling near the base of a blade with its incisors. The blade is held in one forepaw and run through the mouth until the lower part containing the soft meristematic tissue is in the mouth. This is bitten off and chewed while another blade is being pulled out. The operation is performed with great rapidity. Occasionally, the entire blade is consumed. Small pups, not strong enough to pull the grass out readily, often may be seen pulling and tugging at a blade, trying to loosen it from its base. Thistles are bitten off at the base of the leaf and are also eaten from proximal to distal end; thereby the prairiedog is able to masticate the spines on the leaves without being pricked. Because of the practice of eating the basal part of the vegetation first, much of the distal part is cast aside and wasted. Certainly, however, the most nourishing pieces are consumed. Seeds are stripped off the vegetation by running the stem along the mouth until the seeds are brought into it and bitten off. Many seeds are also picked up from the ground and eaten. Roots and tubers are obtained by digging, a process which makes little holes two to three inches deep and about as wide throughout the town. Such holes are most frequently seen during the early spring. During most of the summer scratching for food is too shallow to make a noticeable impression in the earth.

Prairiedogs seldom feed exclusively on one type of plant for any length of time before passing on to another. On August 24, 1950, for example, a young female within 19 minutes ate plants of nine different genera: Schedonnardus, Lappula, Verbena, Chamaesyce, Boebera, Aristida, Carex, Polygonum, and Lygodesmia. Although she spent much time finding and eating spurge (Chamaesyce) seeds, the largest quantity of food consumed was thistle, as entire leaves were devoured at a time.

Some grasses and forbs are clipped off near the base and permitted to fall and dry up without being eaten. Tall vegetation in the middle of the town is entirely removed, but at the edge it is only thinned. The removal of this vegetation is accomplished with great rapidity as the animals move haphazardly from one plant to another. Usually, the vegetation which grows tall enough to be cut down in this fashion is not selected for food.

Vegetation in the middle of the town rarely grows over a foot high because of the clipping and eating activities. In one place a small patch of mullein (Verbascum) had grown over three feet high. It was attacked by the prairiedogs off and on throughout the summer of 1948. Part was eaten; the rest was completely destroyed, and it did not grow up again in 1949 or 1950. The tallest plants in the middle of the town in 1950 were a few stems of needle and thread grass (Stipa), which grew out of a protecting clump of cactus. In the new areas of settlement the grasses were completely cut off only near the burrows, where there was the greatest amount of prairiedog activity. Beyond the immediate vicinity of the burrows, in the newly settled area, the extent of clipping was noticeable only at close range where the cut, dried stems were visible.

By clipping the tall vegetation prairiedogs keep much of the town free of vegetation which might obstruct the view. Since a clear view is important both in their survival from predators and in their social life, this behavior is quite adaptive. Why the presence of tall vegetation should induce this clipping response at some times and places and not at others is not understood at the present time.

Prairiedogs make runways through the tall grass between their burrows (Pl. II, Fig. 1) by trampling the vegetation under foot as they run from burrow to burrow and by the concentrated clipping of vegetation along these pathways. In the older part of the town runways were not visible, since most of the vegetation had been removed, and the animals wandered indiscriminately over the entire area. Even in the new section, where the grass was tall, the prairiedogs did not limit their movements to the runways, but went readily through the thickest grass. The runways were only a by-product of the frequent trips between burrows.

Burrows

The burrow is an important feature in the life of a prairiedog. Not only does it form a refuge from the external environment and a place to rear the young, but it also affects the social structure of the prairiedog society. The intimate relationship between prairiedogs and their burrow systems contributes to the distinct spatial patterns of their social organization. Since the burrows remain essentially the same from generation to generation, they have a stabilizing effect on the organization of the colony.

The exposure of the excavated soil and the denudation of vegetation from the mound and from the surrounding area have many important ecologic effects. The exposed subsoil is affected by weathering and by the encroachment of vegetation. The denuded soil also is especially subject to erosion by water and winds. The size of the denuded area surrounding a burrow is often increased by bison, which use the craters as wallows and consequently expose even more bare earth to the climatic elements.

Kinds of burrows. —The external appearance of the burrows varies considerably. Three general categories based on the excavated soil can be established: (1) a crater-like mound of soil, (2) a mere pile of soil, and (3) practically no soil. The crater-like mound is the largest and most characteristic. Sometimes the mound is as much as three feet high and seven or eight feet wide. The shape of the mound varies somewhat with the mode of its origin and with its age. A distinction between a rim crater and a dome crater is based on the shape and kind of soil in the crater. The rim crater is generally smaller and is carefully formed by the prairiedogs into a crested mound about the entrance of the burrow (Fig 2, top). It is made of the top soil scraped into a pile from the surface of the ground about the entrance and molded by the feet and noses of the prairiedogs to form a compact structure. Sometimes the dirt for this mound is scraped up from an area with a radius of as much as five or six feet. In contrast to the rim crater, the dome crater is often large. It is shaped like a dome, except for the burrow entrance in the middle (Fig. 2, bottom). The mound is composed of pale subsoils or clay which cannot be shaped as effectively by the animals as can the topsoil.

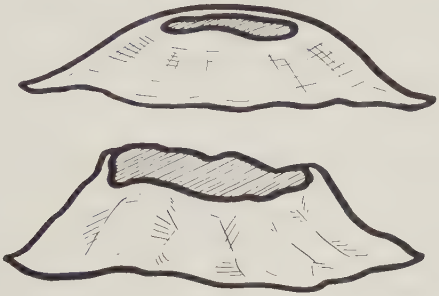

Fig. 2. Diagram of craters around the entrances of prairiedog burrows; top, dome crater; bottom, rim crater.

The differences between these two types of craters apparently depend upon the manner in which the prairiedogs construct their subterranean burrows. The subsoils exposed in the dome craters suggest that the burrow began at the dome crater and that the crater was formed from the excavated soil. When the opening to the burrow comes to the surface some distance away from the original opening, there is at first only a hole with no soil about its entrance. The prairiedogs then scrape the surrounding topsoil and form a rim-shaped crater. A subterranean connection then exists between the two entrances. This underground connection may be plugged with soil and reopened at intervals; hence a connection between the two entrances cannot be ascertained from the nature of the craters alone, except in new areas of only a few burrows. In an old town many other subterranean connections are made which obscure the direct relationship between any two burrow openings.

Those burrows without craters at the entrance are sometimes the result of degeneration of old unattended craters. At other times, a small pile of dirt is left at the entrance of a new, seldom-used burrow. Some of these burrows characterized by an unshaped pile of dirt at the entrance are frequently used and are only in a temporary state of disrepair, whereas others are seldom used. A burrow with little or no excavated soil about the entrance may be the opening of a new entrance from beneath, or, more often, a short, exploratory burrow from which the original dirt has been eroded.

The subterranean passageways of the burrows were not thoroughly explored in this study, although one burrow system was partly excavated. The frequently published diagram (Merriam, 1901) of Osgood's exca-

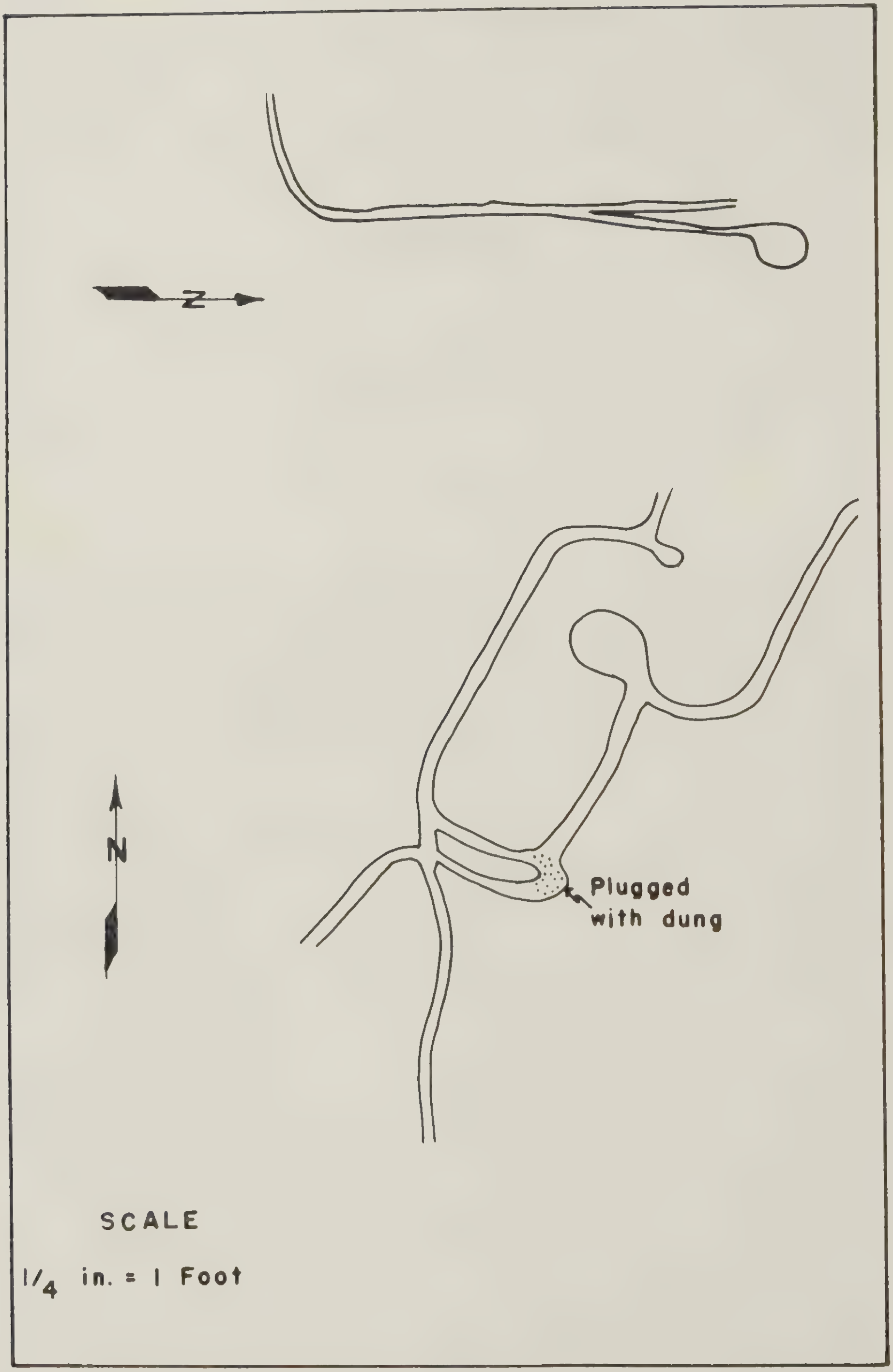

Fig. 3. Diagram of excavated burrow, viewed from the side (top figure) and viewed from above (bottom figure). The nest was in the large chamber.

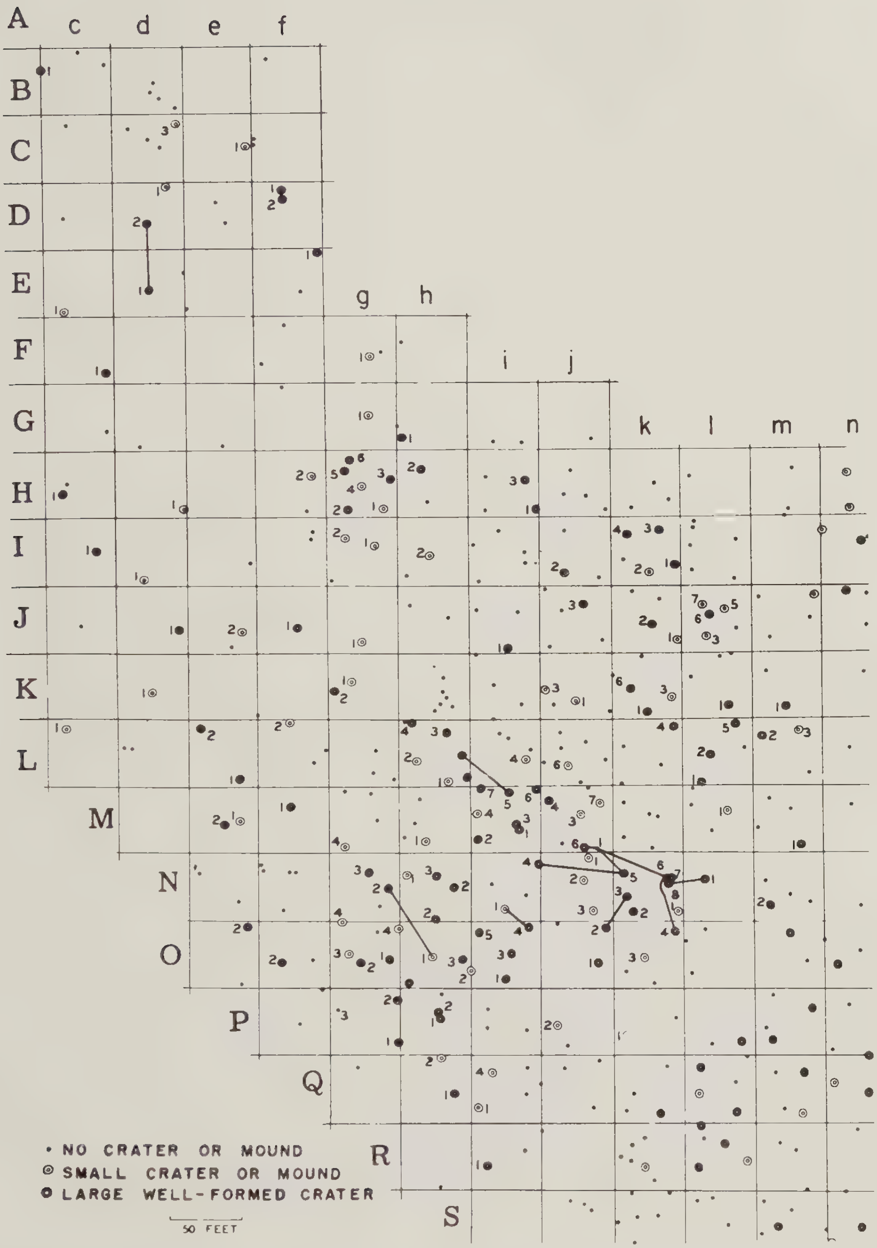

Fig. 4. Burrows on Wards A and B of the Shirttail Canyon town on August 25, 1950. The separation of Wards A and B may be seen by the scarcity of burrows in the longitude of n, with Ward B on the right. The grid pattern illustrates the 50-foot square quadrats used in observing the prairiedogs. Lines connecting the burrows indicate a subterranean connection. Some of the burrows are numbered.

vation of a black-tailed prairiedog's burrow in Nebraska represents a tunnel system very different from the one excavated in Shirttail Canyon. Burrows of related species (Foster, 1924; Whitehead, 1927) have more in common with the burrows studied here. Foster, for example, gave the average depth of the lateral passages as three and one-half feet with seven entrances to the burrow system. This contrasts sharply with the 15-foot depth and single burrow entrance described by Merriam. A diagram of the burrow I partly excavated is presented in Figure 3. Of the 36 feet of the tunnel uncovered, the maximum depth below the ground surface was three feet, except for the nest chamber which was one foot deeper. Only one entrance to the burrow system was found. The uncovered lateral passageways, however, might have led to other openings. The passageways followed a horizontal stratum of sandy loam directly below a stratum of coarse gravel and large rocks. Since most of the soils in Shirttail Canyon are distinctly stratified, tunnels dug in one stratum might easily intersect each other.

The existence of subterranean connections between the burrows was ascertained by watching a marked prairiedog enter one burrow and reappear at another entrance. Figure 4 shows the position of the burrows known to be connected on the study area. These subterranean connections probably are not permanent, but vary from season to season, since the prairiedogs plug them and later reopen them. If I blocked the entrance of a burrow after a prairiedog went down, the same animal usually appeared at another entrance, often with dirt on its claws, indicating that it had probably dug out an old earthen plug. Shortly after the pups came out of the burrows in May the adults frequently were observed digging at the old burrows. I assumed that they were reopening the connections which had been closed for the winter or while the young were in the nest.

The nest chamber in the excavated burrow was 18 inches in diameter and 14 inches in height and was about 12 feet from the burrow entrance at a depth of three feet below the soil surface. The nest was composed of fine, dried grass, which almost filled the chamber. Nesting material is carried into the nests throughout the year by animals of both sexes and of all ages. The animals pick up dried grass, stuff it into their mouths with their forefeet, and carry it into the burrows (Pl. II, Fig. 2). Frequently, nest grass is gathered at a distance from the burrow, often as far away as 150 feet. The carrying of nesting material into the burrows is stimulated to some extent by the discovery of a particularly favorable material or by a period of cold weather.

Numbers of burrows. — In all, 614 burrows were mapped in 1950 on Wards A and B, which together comprise 11.7 acres (Fig. 4). Of the three categories of burrows mentioned previously, 155 were crater burrows, 100 were mound burrows, and the remaining 359 were merely holes. The total number of burrows increased from 540 in 1948 to 614 in 1950. This increase was due partly to the construction of additional crater burrows (89 in 1948 and 155 in 1950) and partly to the digging of more hole burrows (302 in 1948 and 357 in 1950). The number of mound burrows, however, decreased (203 in 1948 and 100 in 1950). The subjectivity in the classification of the burrows may account for some of the difference in the numbers of each type of burrow between 1948 and 1950. Some increase in the number of crater burrows between 1948 and 1950 actually occurred through the development of mound burrows into crater burrows by the activity of the prairiedogs. The increase in number of hole burrows is largely a result of an expansion in the size of Wards A and B from 9.4 acres in 1948 and 11.7 acres in 1950.

The density of the burrows on Wards A and B was 57 per acre in 1948 and 52.5 per acre in 1950. This reduction in density resulted from an increase in the area of Ward A. The density of burrows in the area of expansion, which is included in Ward A, was much lower than in older sections of the town. Burrow density varies considerably throughout a prairiedog town, as well as from one town to the next (Merriam, 1901; Scheffer, 1937; Soper, 1938).

No reliable index can be used to estimate from the number of burrows the number of prairiedogs in a colony. The burrows are more or less permanent, but the number of prairiedogs is not; consequently, any such index would be unreliable, as can be seen by comparing the number of burrows per prairiedog throughout the three years of this study. There were 5.4 burrows per prairiedog in the study area in 1948, 9.6 burrows in 1949, and 4.2 burrows in 1950. These calculations do not mean that one prairiedog is limited even approximately to this number of burrows. The actual number of burrows used by a given individual depends primarily upon social factors and therefore varies according to the social organization of the group. A prairiedog may use any burrow within its home range.

The burrows of the prairiedogs were dug in soils of many different types and textures. Burrows were under large boulders, under roots of trees, and between large buried rocks. Most active burrows were on the floor of the canyon and on the terrace, where the fine-textured soil enabled the prairiedogs to construct deep, continuous passages. Generally, shallow burrows occurred in the marginal regions about the town, where the presence of rocks or impenetrable strata limited subterranean excavations. Prairiedogs apparently do not select certain soil types for their burrows, but begin to dig in almost any kind of soil. Since burrows cannot successfully be made in rocks or loose sand, only short exploratory tunnels are found in these soils. The lack of selection of soil types by prairiedogs agrees with Osborn's (1942) observations of prairiedog burrows in Oklahoma.

Reproduction

Breeding season. — The reproductive cycle of the prairiedog is seasonal, with one breeding season each year. Anthony and Foreman (1951) found that testicular activity begins in early October, but that motile sperm, indicating the approach of sexual activity, is not found in the epididymis until late January. Approximately a month later, in late February and early March, the vaginas of the females open and become swollen. On February 25 and 26, 1950, vaginal inspection of six females revealed two with open vaginas and four with closed vaginas. Between March 3 and 7, 1950, six other females and one which had been previously examined had open vaginas. Mating probably occurs shortly after the vagina opens.

Gestation. — The gestation period is 30 to 35 days (Anthony and Foreman, 1951). Lactating females were observed in Shirttail Canyon near the first of April, about one month after their vaginas were open. One female (No. 16) gave birth to her young on April 3. Most pups on the study area emerged from the burrows within a week of one another and presumably were born about the same time. A pregnant female from another section of the town gave birth to three young on April 16, 1950, while in captivity. Females apparently may have their litters at any time during April, as evidenced by the variation in the size of the young throughout the town.

Lactation. — The period of lactation is approximately seven weeks (Anthony and Foreman, 1951). Throughout this period the nursing pups remain below ground. The first pups out of the burrow were observed on May 11, 1950. The pups of ♀ 16, which were born on April 3, came out of the burrow for the first time on May 17. The pups seldom eat anything solid for the first two or three days after they come out of the burrow, but soon make the transition to solid food. It is not known how long the period of lactation continues, for they may still depend upon the mother for milk while in the burrows at night. Johnson (1927) suggested that "young prairiedogs are probably not able to survive without milk from the mother until after they have attained the age of seven weeks." During the day lactation terminates almost as soon as the pups are out. They frequently attempt to nurse the females outside of the burrows for several weeks after they emerge, but the females seldom remain motionless long enough to permit any feeding. Occasionally, a pup successfully takes hold of a teat while the female is quiet. When she moves off again, the pup is dragged along behind her until it loses its hold.

Growth. — The growth of four captive young prairiedogs from their birth to the age of 103 days has been recorded by Johnson (1927). The weights of his captives increased from about 15 grams at birth to about 350 grams at 100 days of age. Their eyes first opened when they were between 33 and 37 days old. These data resemble those on nine laboratory-raised young studied by Anthony and Foreman (1951). Three young prairiedogs which I raised in captivity in 1950 first opened their eyes at about 30 days of age. Observations on the growth of the free-living pups began shortly after they came out of the burrows, when they were approximately 45 days old. Figure 5 shows the increase in weight of 58 pups until they were about 125 days old. Most of the individuals were weighed at least twice during 1950; the interval between weighings averaged about one month. The graph in Figure 5 reveals no difference in weight between the sexes during the first summer. With the excep-

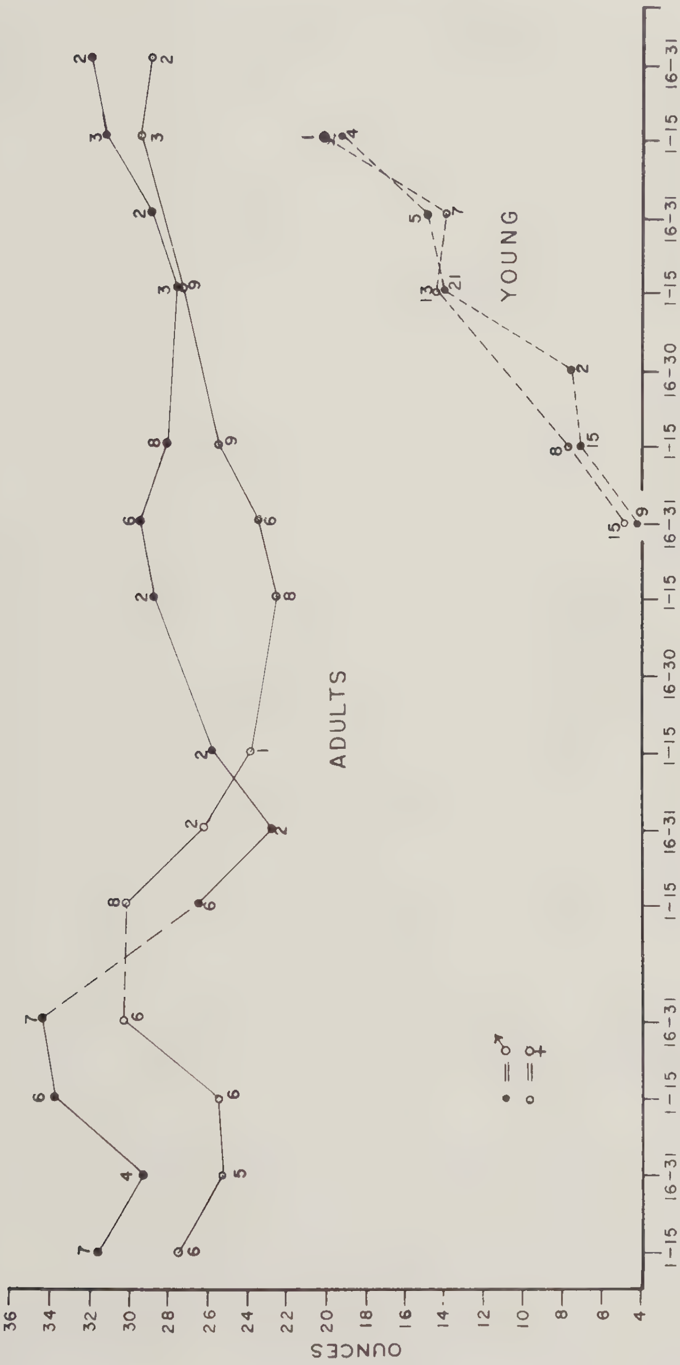

Fig. 5. Weight of prairiedogs in Shirttail Canyon. Numbers indicate the total number of individuals on which each average is based.

tion of a few runts, the pups all have approximately the same weight when they emerge from the burrows. Variation in weight increases as the animals grow older. This may be due to differences in food, social relations, or genetic factors. I have no evidence, however, on the causes of their variability in growth.

Growth of the young prairiedogs continues until they are approximately 15 months old. Young of the year weigh about 20 ounces in August. The rate of growth of the young probably begins to decrease sometime after August because of the onset of winter and a reduction in food. The earliest spring records of weight for yearling animals are those of two males captured April 1 and May 31, 1950. They weighed 21 and 24 ounces, respectively, and both were smaller than older males captured before and after these dates. Apparently, the young of the preceding year do not attain the weight of older, breeding individuals at the time of the breeding season. After the spring vegetation becomes abundant, the yearling prairiedogs increase in weight. In July, when they are approximately 15 months old, they are indistinguishable in weight from most of the older animals (Fig. 5).

The weight of individuals fluctuates considerably throughout the year, the males generally being heavier than the females. Most of the annual fluctuations in weight can be accounted for by the amount of fat the animals accumulate or lose. Relatively little weight is lost during the winter, when their activities are limited by unfavorable weather conditions. In Figure 5 it can be seen that their weights show little decrease between August and early March. Some feeding during the winter probably helps maintain their fat reserves. During the breeding season, when the animals are very active, food is particularly scarce. As a result, weight tends to drop, especially in the males, which are most active at this time. The weight of the females increases later in the spring because of pregnancy, restriction of activities, and perhaps more abundant feeding. Throughout March, consequently, the females tend to weigh more than the males (Fig. 5). While the females are lactating in April and May, they decrease in weight, and during this period the males again weigh more than the females. The weights of both sexes increase throughout the summer, and by late August the adults reach their maximum weight, which averages about 36 ounces for males and 31 for females. Two males and one female, however, weighed as much as 42 ounces at this time.

Longevity. — The longevity of prairiedogs in natural populations is not known; however, age appears to be an important factor in mortality. The loss of individuals older than three years from the population is considerable. The causes for the death of the older prairiedogs are particularly interesting, since senility in a natural population in not common.. Prairiedogs have been known to live in captivity as long as eight and one-half years (Young, 1944). A population of prairiedogs in Texas persisted for seven years without any reproduction (Stockard, personal communication). These figures show that the potential longevity of prairiedogs is rather high; however, in nature it is very likely reduced. For example, two males that were probably little over three years old returned to their burrows in the late summer in 1949. They had not accumulated much fat during the summer, partly because they were restricted to an area poor in vegetation and partly because they did not spend much of their time eating, since they remained in their burrows most of the day. Judging from their physical condition, I predicted that they would not live throughout the winter. Neither of these old males was seen again. For another example, a male that had been dominant during 1948 and 1949 and was therefore at least three years old was observed again in February, 1950. His dominant position had been usurped by an invading male. The two males lived at peace for a time, but when the old male began to take an interest in the females, a conflict arose between the males, and the older one was either killed or driven from the area. These examples do not afford sufficient evidence that the male died of senility, but they do indicate that age is a factor in mortality.

Females may live longer than males under natural conditions. Six females caught as pups in 1948 were living on Ward A in 1952. The fact that four of these six females were lactating indicates that at least three litters may be raised by a female during her life span. All except one of the six females had litters in 1950. The female which did not produce young in 1950 showed no evidence of lactation in 1952. Of the total population only three males were observed to attain the age of three years. There are no records of males living four years.

Reactions to Physical Environment

Much of the behavior of prairiedogs is periodic, corresponding with periodicities in the physical and biotic environment. Some of their activities are correlated with the daily rhythm; others are affected by the seasonal rhythm of the environment.

Daily periodicity. — Light intensity determines many of the activities of prairiedogs. This is particularly apparent in their daily periodicity, as they are entirely diurnal. The importance of light is also indicated by their reactions to the presence or absence of sunshine. This relationship is most evident during the winter months; when there is snow on the ground they come out of their burrows only on sunny days. The effect of sunshine is also noticeable in the relative shyness of the prairiedogs on cloudy and on sunny days. On sunny days they are much less shy, bark less at the observer, run down their burrows less often, and stay in their burrows for a shorter period of time than on cloudy days. In the spring this dependence on sunshine becomes less precise. By early summer some animals are always active during the daylight hours, independent of the sunshine.

In their daily activity prairiedogs usually come out of their burrows near sunrise and return to them within half an hour after sunset. These

TABLE VI
Time of emergence from burrow in relation to time of first sunshine on Ward A an to minimum temperature. Asterisks indicate dominant animals.

Date	Number and Sex of Animal	Time First Prairiedog Emerges from Burrow	Time Sunshine First Strikes Ward A	Maximum Temperatures for the Day (degrees Fahrenheit)
July, 1949				
20	♀ 17	5:21	4:55	57
21	♂ 6*	5:20	4:57	57
23	♀ 14	5:00	5:00	50
24	♂ 6*	4:47	5:00	58
25	♂ 6*	4:48	5:27	47
28	♂ 24*	5:03	5:04	56
29	♀ 17	5:23	Cloudy	70
30	♂ 50	5:04	5:06	59
31	♂ 24*	5:06	5:08	52
August, 1949				
1	♂ 6*	4:58	5:09	49
3	♂ 25	5:15	5:10	56
4	♂ 24*	5:10	5:10	61
5	♂ 10*	5:13	5:34	60
6	♂ 6*	5:04	5:11	62
8	♂ 4	5:10	5:13	53
9	♂ 24*	5:29	5:16	60
10	♂ 50	5:30	5:19	56
11	♂ 27*	5:25	5:17	60
12	♂ 6*	5:18	5:20	61
14	♂ 6*	5:20	6:03	54
15	♂ 25	5:19	5:21	53
16	♂ 6*	5:08	5:21	56
17	♂ 6*	5:17	Cloudy	55
18	♂ 6*	5:12	Cloudy	52
19	♂ 6*	5:26	5:28	46
21	♂ 25	5:26	5:27	43
22	♂ 6*	5:31	5:30	51
23	♂ 25	5:30	5:30	49
24	♂ 6*	5:43	Cloudy	..
25	♂ 6*	5:35	6:04	..
26	♂ 6*	5:33	5:38	..
27	♂ 6*	5:36	5:35	..

strictly diurnal habits are reflected in certain of their adaptations. The lenses of a prairiedog's eyes are almost orange and the retina consists entirely of cones (Walls, 1942). Adaptations to strong light make the animals unsuited to crepuscular or nocturnal activity. On several occasions prairiedogs were released from traps in the evening under light conditions which only slightly interfered with my own vision. The prairiedogs, however, acted as if they were almost completely blind and found their burrows apparently by odor and kinesthesis. It was indeed strange to watch an excited prairiedog grope blindly about the crater of a burrow searching for the entrance, in contrast to the direct plunge it would have made during hours of sunshine.

The time at which prairiedogs first appear from their burrows on summer mornings seems to have little relationship to such environmental factors as sunshine and temperature. In an effort to ascertain the relationship between the time of the animals' first appearance above ground and the time when the sunshine first reached the study area in full strength over the surrounding hills or through clouds, records of both were collected for 43 days. It can be seen from Table VI that the time when the prairiedogs first emerged from their burrows in the morning varied greatly (from 4:47 a.m. to 5:43 a.m., within one month), and that the time of emergence varied widely before and after the sunshine reached the study area. The wide range in the time of emergence from the burrows indicates that prairiedogs do not come from their burrows in response to the first sunshine that reaches the town. Table VI also shows that the animals came from their burrows in the morning over a wide range of time after nights with low as well as with high minimum temperatures. These wide ranges of time again fail to show any close relationship between temperature and time of first emergence from the burrows. Although prairiedogs come out of their burrows only in hours of daylight, there is no obvious environmental factor which signals its arrival to the animals in their burrows.

The time at which prairiedogs appear from their burrows in the mornings is also difficult to attribute to an internal physiologic periodicity. During the winter I have seen them come out of their burrows on dark, foggy days, look around for a minute, and return to their burrows for several hours. Perhaps in the morning the animals wake up, crawl part way up the burrow, and then either come out or return to their nests, according to the amount of light or existing weather conditions. Hunger may stir them to activity in the morning. Social factors may also influence the time at which they appear from their burrows. The dominant male of each of four territories was the first individual to appear on the study area 37 times of the total 43 mornings (Table VI). These records cover only the first individual out in the entire study area; additional observations on the individuals which appeared subsequently show that the second and third prairiedogs out were usually other dominant males. It is very likely that the dominant males come out first in the morning in order to guard their territories against invasions from neighboring individuals. Invasions of unguarded, adjacent territories were common at this time of day. Other social factors which might influence the appearance of prairiedogs are the vocalizations of those first to appear. If the calls of animals already out could be heard by those below, the latter might be signaled that the activities of the day had begun. Certainly, once an individual did come out and see others about him, he would likely remain out for the day. Furthermore, the departure of some individuals from a common nest might arouse their associates to activity.

Table VII
Numbers of prairiedogs visible at half-hour intervals on three days in 1950, Ward A. The total population consisted of seventeen individuals. Parentheses indicate disturbance shortly before the count was made.

Time	Number of Individuals		
	July 19	July 31	August 2
A. M.			
5:00	0	0	...
5:30	3	17	5
6:00	11	17	13
6:30	7	17	14
7:00	15	16	12
7:30	...	...	...
8:00	(7)	...	(6)
8:30	14	10	14
9:00	17	7	13
9:30	12	8	11
10:00	13	7	12
10:30	16	13	7
11:00	14	12	8
11:30	13	13	9
P. M.			
12:00	9	...	...
12.30	...	...	...
1:00	(9)	10	7
1:30	13	13	9
2:00	15	8	10
2:30	14	12	10
3:00	14	10	6
3:30	11	11	7
4:00	13	13	9
4:30	14	16	8
5:00	15	12	11
5:30	...	...	...
6:00	...	...	9
6:30	...	17	12
7:00	2	0	6

Once the prairiedogs have emerged from their burrows in the morning, no further periodicity in their activity can be detected until evening. A census was made every half hour for three days on the number of animals out of their burrows in one small, socially distinct area, which was inhabited by 17 animals. This census indicated no general retreat to the burrows at any particular time during the daily period of activity (Table VII). The small number of animals counted at some periods of the day was most often due to their feeding activities in the tall grass at the edge of the town, where they could not readily be seen. The larger numbers seen in the morning and toward evening indicate a slight rhythm in their behavior. When they first come out in the morning, they generally remain in the vicinity of a few main burrows to feed for a while. Gradually they disperse, many going to the burrows toward the periphery of the town, where the grass is taller. A few individuals remain in the grass during most of the day, but shortly before going into the burrows for the night they again concentrate about the major burrows in the middle of the town. Additional records of individuals watched throughout an entire day failed to indicate any rhythm. From entirely subjective observations, I did seem to notice more concentrated feeding efforts just after sunset, immediately before the animals went into their burrows for the night. Occasionally, they fed intently in the morning when they first came out of the burrows, but there were so many variations in their behavior at this time that no consistency was ascertained.

Reactions to weather. — Prairiedog activity is reduced only on the hottest summer days. Limited observations of their behavior when the air temperature was over 100° F. indicate that they did not make use of the few shadows on the study area, but made frequent trips into their burrows, presumably for the purpose of cooling off (Table VIII). On cooler days they spent only 15 per cent of their active day inside burrows in contrast to 42 per cent of the time spent in burrows when the temperature was over 100° F. Extremely hot days, however, are relatively rare in Shirttail Canyon, and the activities of the prairiedogs are little curtailed by temperatures lower than 100° F.

TABLE VIII

Lengths of successive periods (in minutes) spent by prairiedogs outside of and within burrows. August 22-23, 1949, Ward A. Periods which are starred (*) were spent inside the burrow. On these dates, the temperature of the air was 100° F., that of the ground surface 113° F., and that in a burrow one foot below ground surface 74° F.

Individual	August 22, 1949	August 23, 1949
♂ 6	10 - 15* - 10 - 13* - 13 - 1* - 2	8 - 1* - 6 - 10* - 15 - 7* - 8 - 6*
♀ 14	30* - 15 - 4* - 8	19 - 9* - 9 - 7* - 15
♀ 16	23 - 10* - 5 - 9* - 21	16 - 13* - 16 - 7 - 13
♂ 25		14 - 9* - 28 - 16*

When the individual remained in a trap exposed to the sun for several hours on a hot day, it showed evident signs of overheating. Saliva came from its mouth and wet the fur about its muzzle and breast. The animal crowded into the shadow of the trap door after its initial struggles to escape had ceased. When the toe of an animal which had been in a trap for some time was clipped, blood spurted out of the stump in a fine stream, in contrast to its slow dripping on cooler days or immediately after capture on a hot day. Although no body temperatures were taken, the fact that there was no trap mortality on hot days indicates that prairiedogs either have a delicate heat-regulating mechanism or can tolerate high body temperatures.

Prairiedogs usually do not come out of their burrows while rain or snow is falling, but do come out shortly after it has ceased. They often burrow up through snow and run about on it when the sun shines again. During summer and late spring showers, rather heavy rainfall, is necessary to drive the animals into their burrows. They are often very active immediately after rain, working the moist soil about their burrows into well-shaped craters. This activity has been wrongly considered a forecast of rain. Heavy fogs and mosts usually keep the animals in their burrows, particularly during the cool spring and early in the morning during the summer.

Seasonal variations in activity. — Seasonal changes in the behavior of the prairiedogs are associated with their reproductive cycle, with dormancy, with variations in feeding, and with accumulation of fat. Their reproductive cycle and their changes in weight due to growth and the accumulation of fat have been discussed under reproduction. Only a few observations were made on dormancy and on variations in feeding behavior throughout the year.

My winter observations of prairiedogs in Shirttail Canyon were limited to late February and early March of 1950. The temperatures in the latter part of February often went above 60° F., which, combined with brilliant sunshine, made the weather quite warm for this season. There was no precipitation during most of the latter part of the winter. The prairiedogs were very active during this time of year because mating was in progress and the weather was mild. Early in the spring the temperatures were lower, and there were frequent snowfalls and clouds. The prairiedogs continued to be active except on days when it was snowing and cloudy. They seldom remained in their burrows for more than a day or two at a time. Other observers in Wind Cave National Park have reported that the prairiedogs are out at intervals throughout the winter. In 1949 Louis Kirk, park ranger, saw them active even two days after a "heavy snow and extreme cold (-18° F.)." Cahalane (1947) also mentioned seeing them out of their burrows during January and February in western South Dakota. In the lower latitudes of their range winter activity outside the burrows is probably still more frequent (Hollister, 1916).

Periods of winter dormancy and decreased activity have been observed in captive prairiedogs. Two captives from the Shirttail Canyon colony were kept at Ann Arbor, Michigan; one during the winter of 1948 and one during that of 1950. Both of the animals were active at room temperatures throughout the winter, although their daily activity was much reduced during December and January. Young (1944) kept two prairiedogs in captivity for a period of eight and one-half years, during which time he observed that one animal (C. gunnisoni) went into hibernation for the winter, whereas the other (C. ludovicianus) slept for short intervals of three or four days throughout the winter. Stockard (1930) found that two captives of C. leucurus become dormant at room temperatures during the winter. These observations suggest that hibernation is less complete in ludovicianus than it is in related species.

Short periods of dormancy during the winter seem to be characteristic of C. ludovicianus. The animals apparently hole up during the worst weather, but come out at intervals when the weather is more favorable. Throughout May a foggy or rainy day may keep them down all day, but after the latter part of that month some prairiedogs are out part of each day until winter weather again drives them below. There is no reduction of activity during the summer months in C. ludovicianus, in contrast to C. leucurus, which goes into estivation during July in Wyoming (Stockard, 1930).

These observations of activity throughout the winter, when the temperatures are far below freezing, indicate that prairiedogs show no particular aversion to cold temperatures. Their thick winter pelage serves as an effective insulator against excessive heat loss. Cold temperatures, however, combined with lack of abundant food and cloudy days, probably have the effect of decreasing their activity. Young animals which were accidentally left in a trap during the night when the temperature went below 40° F. often were found in a comatose state in the morning. Warming them in the sun and giving them a little milk usually brought them out of this state. It is possible that one small pup died from such an experience after it had been treated for several days. The underlying cause of the death of this individual, however, might have been an alimentary disorder.

Prairiedogs feed heavily on the fresh vegetation shortly after it comes up in the spring. This voracious feeding continues throughout the summer as long as there is abundant food. As a result, large fat reserves are built up (Fig. 5). During the winter lack of abundant food appears to be correlated with a diminished appetite. When the animals were observed in February and March before the spring vegetation came up, they merely nibbled at the remaining vegetation. Observations of two captive prairiedogs made it possible to follow these fluctuations in their feeding habits more completely. Favorite foods were always available to the captives, but their heavy feeding of August and September decreased considerably by December and January. In these months only a few sunflower seeds were eaten each day, and the number of fecal pellets per day was reduced to three or four small, dry ones.

The seasonal distribution of precipitation also may produce variations in the behavior of the prairiedogs. Heavy spring snows reduce their activity, although the animals frequently dig out of their burrows through several inches of snow. Feeding is hampered by the cover of snow, and the animals move about on the surface with difficulty. Often they merely sit at the burrow entrance or go off a few feet to tunnel for food through the snow. Trips from one burrow to another are made with little deviation from a straight line.

Pregnant and lactating females frequently were observed eating snow. Since snow is the primary source of water during the early spring, when most of the vegetation present on the town is dry and dead, the breeding season may depend upon its presence. Lindeborg (1950) has suggested that the presence of free water in the environment may be an important factor in the control of the breeding season in many mammals. The availability of water in the form of snow may account for the early time of year in which mating occurs. It seems that the young are born too early in the season to afford them ideal conditions when they first come out of the burrows, as there is little available food. More critical stages in their development, however, may exist while they are still within the nest and dependent entirely upon the milk of their mothers, which in turn may depend upon the amount of available water. Later spring rains seldom furnish any free water, as it quickly runs off the surface or is absorbed into the dry soil.

During the summer the moisture in the food of the animals and their metabolic water apparently supply them with sufficient amounts for their physiological processes. They never were observed to drink any of the free water which was occasionally present for a short time after a rainfall in the summer. When I placed water out for them, they quickly filled the vessel containing it with dirt.

Relations with Other Animals

Prairiedogs are the prey of many reptiles, birds, and mammals. The most common of these potential predators in Shirttail Canyon were rattlesnakes (Crotalus), bull snakes (Pituophis), golden eagles (Aquila chrysaëtos), red-tailed hawks (Buteo borealis), coyotes (Canis latrans), and bobcats (Lynx rufus). Only a bobcat and eagle left any direct evidence of success in preying upon the prairiedogs during this study. The other predators seen in the canyon either were not hunting for prairiedogs or were unsuccessful in their attempts to capture them.

Predation. — Four rattlesnakes were seen in Shirttail Canyon during the entire study. Three of these were found at the edge of the town, in prairiedog burrows which were seldom used by the prairiedogs. These were small snakes that probably could not have swallowed young prairiedogs even if they had killed them. A large rattlesnake found in some brush along the stream bed might have been able to eat a small prairiedog; however, its stomach was empty. The period during which the pups serve as prey for snakes must be short in Shirttail Canyon, because the snakes are probably still hibernating when the pups are small. By the middle of June most of the pups weigh about six to eight ounces and are probably too large for many rattlesnakes. It is likely that ground squirrels and deermice, which also live in the town, are the principal items of prey of these snakes.

The attitude of the prairiedogs toward rattlesnakes gives a further clue to their importance as predators. On two occasions I tied a string about a rattlesnake's neck and staked it out in the town. Although the snake's primary effort was to escape, the prairiedogs came up and fed within a foot of it, often within the length of the string. They were curious about the snake and approached it cautiously, sometimes calling as they ran off and then returned to the snake. Prairiedogs never barked at snakes. When one rattlesnake was released, a pup followed it and even pawed at its tail as it crawled away. Such behavior can hardly be characteristic of a prey species toward its predator.

Only one bull snake was seen in the Shirttail Canyon town. It was caught emerging from a prairiedog burrow, but showed no evidence of having recently eaten the inhabitant. Later, this snake was staked out in the town, and the prairiedogs reacted to it as they reacted to the rattlesnakes. Probably bull snakes, like rattlesnakes, prey upon prairiedogs only for the short period from the time when the snakes come out of hibernation until the prairiedogs are too large for them.

A number of hawks were seen at intervals about the canyon. Most of them were of small or medium size and probably offered no threat to a full-grown prairiedog. Occasionally, larger red-tailed hawks and eagles were seen over the town; and, although they sometimes swooped low, I never saw one dive at a prairiedog. That they do so was evidenced by tracks in the snow on April 30, 1950. A prairiedog had emerged from a burrow and had wandered aimlessly on top of the snow about 125 feet from its burrow, when an eagle dived on it. A little blood and the absence of prairiedog tracks leading from the scene indicated that the eagle had made a kill. The presence of many eagles about the canyon in the winter and early spring suggests that such kills are common. Early in the summer the eagles disappeared and did not return to the canyon until late summer, when a few were present. Hawks were not frequent visitors to the canyon.

Prairiedogs show much fear of predacious birds, in contrast to their behavior toward snakes. They have a particular vocalization which signals the approach of a hawk or an eagle. This is a quick, short series of barks, which apparently acts directly as a stimulus to send the prairiedogs running to their burrows, even without perceiving the source of danger. Once at his burrow entrance, a prairiedog sits up and watches the bird as it hovers about, allowing it to come quite close before he dives into the burrow. When the eagle or hawk has passed by, prairiedogs respond vocally with a call, which on this occasion serves as an all-is-well signal. The approach and departure of a hawk or an eagle could easily be detected by the observer from the prairiedogs' vocalizations. Even the eye of the prairiedog seems adapted to better perception of such enemies, since the optic disk is oriented horizontally far above the optic axis to permit unimpeded vision from the lower part of the retina (Walls, 1942: 180). Further, the resolving power of the entire retina of the prairiedog is as keen as the fovea of many other animals (Walls, 1942: 312). Thus, the prairiedog is well adapted in both its social behavior and its morphology to cope with its aerial enemies.

Coyotes were frequently seen and heard in the canyon, but none was observed stalking a prairiedog, nor was there any evidence to suggest that they preyed upon the prairiedogs. Their tracks were never seen in the snow about the town in the winter, when one might expect coyotes to be particularly alert for active prey. When they crossed the town, they did not pay much attention to the prairiedogs. A coyote would have little chance to catch a prairiedog in the center of the town, though it might successfully stalk one near the edge. The difference in daily periods of activity of the prey and the predator probably operates in favor of the prairiedogs.

Prairiedogs react toward the coyotes in much the same manner as they do toward human beings. Upon perceiving the coyote, they run to their burrows, sit up, and bark until the coyote has come quite close, whereupon they go below. The barking is steady, varying in intensity and frequency in accordance with the actions of the coyote. The barks are not quick and short like those given for a hawk, and it seems that the danger must be perceived before all the prairiedogs run to the burrows. The bark alone does not serve as the stimulus for retreat.

Bobcats were observed in the canyon three times. The first time was on August 11, 1949, when one was seen carrying a large prairiedog in its mouth along the canyon floor. When frightened, the cat dropped its prey and ran across the town, disappearing in some rocks on the other side of the canyon. The prairiedog was an adult male and was still warm. On another occasion a bobcat was seen running up the canyon slope through the trees beside the edge of the town, where it presumably had been stalking prairiedogs. The third time was early in the morning, when a bobcat crossed the study area while I was in the blind. It was not hunting, but merely crossed the town, stopping here and there to smell or roll around in the grass. These observations show that bobcats occasionally do prey upon the prairiedogs.

Prairiedogs react toward bobcats as they do toward coyotes. On one occasion, however, the bobcat's sudden appearance over the edge of the town evoked from the prairiedogs a rapid bark, similar to the hawk-warning bark. This change in their bark seems to be due to the rapidity with which danger appears, rather than to a specific type of danger.

Badgers (Taxidea taxus) were present in neighboring prairiedog towns in Wind Cave National Park, but were not in the Shirttail Canyon town. Some enlarged burrows within the town suggest that they had been in the canyon before the study began. It is possible that they may soon return to Shirttail Canyon.

Predation. — The amount of predation in Shirttail Canyon is not known, but the rare evidence of it and the low mortality of the prairiedogs under observation indicate that it must have been slight while the study was in progress. Perhaps the observer's presence kept some of the predators away, though this is doubtful. Predation may have taken a greater toll of the animals during part of the year when observations were not made. It is further possible that the study area was in a better position to guard against predators than were other parts of the town. The predators may have found their prey elsewhere in the town, thus relieving pressure on the study area. Whatever the situation, I doubt if predation accounts for much of the mortality of the prairiedogs upon the study area.

Although the prairiedogs are subject to predation at all times, it is likely that they guard effectively against it most of the time. Their dense colonies, with the great number of eyes ready to perceive danger, and their vocalizations which signal to the other members of the colony are effective in alerting all the inhabitants; once alert, they have safe refuge from most enemies in the abundant burrows. These elements of the colony are basic to the survival of the prairiedogs. At any time when the prairiedogs are without these protective elements, mortality is high. A prairiedog caught by an eagle, for example, was alone on top of the snow. It had no neighbor to warn it of the eagle's approach; and even if it had been warned, it probably could not have reached the burrow 125 feet away. Thus, predation may be especially heavy during the winter. In the summer, when some prairiedogs are migrating, they are again without the protection afforded by other individuals and by the burrows. For example, I caught an adult male merely by running him down in a field where he had wandered outside of the town. Other prairiedogs which had spread into a new area often had to run more than 200 yards to their old burrows in order to escape from me. During the spring, before the vegetation of the town comes up, prairiedogs often forage far from their burrows and may be exposed to predation at such times. Occasionally, they are driven out of a settled area by other prairiedogs and are caught without a ready burrow for refuge. It is probable that upon such occasions predation takes its greatest toll.

Other relations. — Many animals are associated with the prairiedogs. Some of these associated species serve as food for the prairiedogs, others use the prairiedogs as food; some parasitize the prairiedogs, others benefit them; some dwell in their burrows, others merely pass over the town in their movements. All enter the complex of the prairiedog community, withdrawing from the integrated whole and contributing sustenance to it. The community aspect of the prairiedog town merits a brief description.

Prairiedogs are almost strictly herbivorous, although at times they eat insects (Kelso, 1939; Whitehead, 1927). Frequently, prairiedogs chase grasshoppers, but I have never seen insects captured. Grasshoppers are not an important item in their food. I have seen the prairiedogs smell ants and beetles, but I have never seen one eaten. On March 22, 1950, I put out a fresh carcass of a harvest mouse (Reithrodontomys) on a prairiedog's crater. The carcass was initially ignored, though several hours later, one individual picked up the carcass and nibbled on it, but then discarded it and did not return to it. At this time of year there was very little vegetation available. Such lack of interest in animal food indicates that flesh probably is of little importance in the diet of prairiedogs.

Parasites are frequently found on prairiedogs. The most common are fleas (Opisocrostis hirsutus), mites (Atricholaelaps glasgowi), and ticks (Ixodes sp.).[3] No quantitative measures were made of the abundance of parasites, but fleas and mites often were seen in great numbers while the prairiedogs were being handled. Ticks, on the other hand, were encountered only a few times on the prairiedogs. The numbers of parasites seemed to differ from individual to individual and from time to time on the same individual. Parasites cause some discomfort to the prairiedogs, which often scratch or bite themselves. Occasionally, a prairiedog leaped into the air and then rolled in the dust, apparently trying to rid itself of some annoying parasite.

Various species of insects, reptiles, and mammals use the prairiedog burrows as nests or refuges. The insects often live in the same burrows with the prairiedogs, but the mammals use burrows less frequented by the prairiedogs, and then only for temporary refuges. This is particularly true of deermice (Peromyscus maniculatus) and cottontail rabbits (Sylvilagus). Ground squirrels (Citellus tridecemlineatus) and field mice (Microtus ochrogaster) also enter the burrows on occasion. It is not known whether any of these mammals make nests in the burrows or merely use them for refuges. Ground squirrels have their own burrows and usually run to them, unless they are hard pressed, when they go down a prairiedog burrow. Deermice at times are abundant on the town, but usually they make their nests under rocks. Prairiedogs react to other small mammals with indifference or mild curiosity. The prairiedogs under observation occasionally tried to investigate the ground squirrels, but the latter usually ran away. On one occasion a pup walked up to a young rabbit, smelled it, and then chased it about, while the rabbit easily pranced away from the pup. The rather tame rabbits and prairiedogs about the camp completely ignored one another, though they often fed close together. Rattlesnakes and bull snakes were seen down the burrows of prairiedogs. There were no burrowing owls (Speotyto) in this town.

The prairiedog community is frequented by many other mammals which pass through the canyon or live about its sides. Some of the mammals, such as the red squirrels (Tamiasciurus), chipmunks (Eutamias), and porcupines (Erethizon), probably do little to disturb the prairiedogs or to modify their homes. Others, such as the mule deer and white-tailed deer (Odocoileus) and elk (Cervus), which enter the town at night, feed upon the abundant forbs. The open area of the town seemed to be the meeting ground for the Cervidae on some occasions. What they found on the town to attract them is not known, but their frequent presence suggests that some tasty forbs had brought them into the opening to feed before they moved into the grasslands and forests.

[3] Identification of the fleas and ticks was made by Glen M. Kohls, senior entomologist, U. S. Public Health Service. The mites were identified by E. W. Baker of the U. S. National Museum.

A third group of mammals was definitely drawn to the town for one reason or another and spent much time on it — the antelope (Antilocapra) and the bison (Bison). Antelope often were observed in the town during the day, singly or in small groups. Sometimes they spent most of the day there, feeding or lying in the shade of the scattered pine trees. Their presence on the town can be explained partly by their food preferences, which include forbs of many varieties. On the town they found abundant forbs, which only rarely grow in the well-sodded grasslands. One afternoon an antelope foraged through the study area and ate nearly half of the blossoms of beardstongue, which were untouched by the prairiedogs. Such feeding habits further modify the vegetation of the town, which is already altered by the prairiedogs.

The prairiedogs did not object to the presence of the antelope, once they were recognized as harmless. Often prairiedogs fed within a few feet of one or peered from the burrows as it grazed nearby. It was only when antelope first approached the town and were not recognized immediately or when they ran through the town that the prairiedogs were alerted and barked at them.

A bison herd, numbering 150 to 300 animals, occasionally passed through the canyon. Sometimes it stayed for a week and at other times it remained for only an hour. Once in a while a small group or even a single old bull came on the town. It was common for the herd to pass through the town on the way to water farther up the canyon and then to return to rest among the prairiedog burrows. A herd of 300 bison spending the afternoon on an area of 40 to 80 acres soon makes the town look like a stockyard. Their wallows, as well as their dung, were signs of their presence and abundance. The denuded earth about the burrows formed a favorite place to begin a wallow. The bison would approach a well-formed crater, paw at it, dig it with his horns, and then lie down and wallow, frequently filling the burrow and spreading the crater. Such dust baths increased the size of the denuded area about the burrow and frequently made a deep depression in the surface where water collected and stood for several days after a rain. The vegetation of the town was further modified by the herd's feeding while visiting the town. Probably the bison also found several varieties of edible forbs which did not grow elsewhere on the range.

The prairiedogs reacted toward the bison much as they did toward the antelope. The greater size and number of the bison and their more violent movements disturbed the prairiedogs more than the delicate antelope did. While the bison were wallowing or sparring with one another, the prairiedogs frequently remained in their burrows; however, when the bison were grazing or ruminating quietly, the prairiedogs showed no fear of them and fed undisturbed within a few feet. The damage frequently done to their craters by the wallowing bison was generally repaired with much diligence by the prairiedogs. Particular craters, however, became favorite wallowing sites; and in the face of such constant destruction, the prairiedogs occasionally relinquished the burrows to the bison. Thus, the town was spotted by the denuded areas of the wallows, which exposed the bare earth to erosion by wind and water and to the encroachment of forbs.

Reactions to Observer

The presence of an observer affects the behavior of wild mammals in many ways. By inhibiting some responses which the animals would ordinarily make in his absence, he may fail to observe the full scope of their behavior. On the other hand, some patterns of behavior are exhibited only in the presence of the observer. Reactions to him may vary among individuals and among groups, with age and with the type of disturbance. Unfamiliar objects on the town, such as blinds and traps, are slowly accepted by the inhabitants. In general, prairiedogs react cautiously to the observer, showing patterns of alertness and fear when they are aware of his presence.

Observer. — Prairiedogs run to their burrows and bark when an observer walks into their town. As he approaches, they crouch low over the burrow entrance and continue to bark. With every bark, their tails jerk vertically in squirrel-like fashion. Gradually, they conceal their bodies in the burrows until only their heads and finally just their eyes protrude from the entrance. Then they suddenly disappear into the burrows, barking from below. Once they retreat, they usually remain underground for long periods.

This pattern of behavior varies from individual to individual and from time to time, but generally it is characteristic of most of the prairiedogs. Even after the prairiedogs watched me approach the town many times, they continued to act in the same cautious manner. The greatest variations were not in the pattern of reaction, but in the threshold of the stimulus to release it. As the prairiedogs became familiar with my presence, I was able to approach them closely before they showed alarm. Then, within a few minutes after I entered the blind, they reappeared from their burrows.

Their reactions also varied in accordance with the nature of the disturbance created by the observer. If I ran rapidly across the town, they disappeared down their holes much sooner than they did if I merely walked. On the other hand, when I worked quietly in one section of the town, the prairiedogs often foraged close by, unconcerned. Frequently, however, one or two shy individuals kept barking at me from distant burrows throughout the course of my activities. On one occasion, an individual barked at me for an hour from a burrow about 150 feet away. Every time I moved, this individual increased the frequency and intensity of its barks. This vocal report of my movements apparently kept all the others in their burrows.

Though little attempt was made to tame the prairiedogs, some became very familiar, and others were always very timid. The bold individuals seldom ran down their burrows when I passed by within 15 to 25 feet; if they did, they soon reappeared. Nor did they customarily bark at me. Instead, they sat silently on their burrows and watched me pass. These tame animals were often caught in the trap. When they were released, they would run down the burrow, turn around, and immediately come out and again eat the oats in the rebaited trap.

Not only was there a difference in the reactions of individuals, but also different parts of the colony and even different social groups varied considerably in their behavior toward the observer. Those parts of the colony which had the least contact with the observer tended to be most irritable, but familiarity with the observer was not the only factor involved. I crossed one section of the town several times a day, and on each occasion great caution was exhibited by the inhabitants. One social group of prairiedogs that occupied an area immediately adjacent to the observation tower was always more irritable than another group in the adjoining area. Many of these variations in group behavior are believed to have been due to the excessive irritability of one or two individuals, whose continuous barking affected the other animals in the group.

Age of the animals is another factor which produced variations in prairiedog reactions to an observer. When the pups first appeared from their burrows, they acted bewildered and seemed unaware of the meaning of the warning barks. As a result, they often remained on the craters long after the adults had gone down. In a few days, however, they appeared to learn the meaning of the barks and became easily excited by them, even more so than the adults. At this stage, they darted into their burrows at the slightest danger. It took about two weeks for this hypersensitivity to wear off. At the end of this period they became more curious and began to show differences in personality. They also began to bark at things strange to them and even seemed to bark at nothing. Because of their curiosity they often remained aboveground longer than the adults. This period of curiosity blended imperceptibly into their mature individual and group patterns of reaction.

Blinds. — The elevated blind was a conspicuous object on the open grassland, particularly when the burlap sides flapped in the wind, but it seemed to hold no terror for the prairiedogs. Some of them frequently foraged beneath and around it. Their reaction was the same when I was in the blind, despite the disturbance I had just created by walking through the town to reach it. Their indifference to my presence in the blind permitted me to move about quite freely and even to make a considerable amount of noise without disturbing them; however, a scrape of the chair, a flap of a notebook paper, or a quick movement usually alerted them, although it did not cause them to bark. In one or two minutes they would then resume their usual activities. The blind became a permanent object on their landscape, and they probably became adjusted to it.

Whenever the automobile was used as a blind, the prairiedogs regarded it as they did the elevated blind. Movements of the automobile disturbed them somewhat, but not as much as did a person on foot. Some of the bold individuals, associating the car with a gift of oats thrown to them, came running up to the car and searched around for oats. This association with food was never established with me when I was on foot. Later in the 1950 season, however, the pups frequently gathered around the blind in search of oats after I had entered it.

Traps. — The reactions of the individuals to traps varied considerably. Most prairiedogs always held the traps in suspicion. Some individuals never approached the traps closely enough to be influenced by the bait. Others associated the traps with the bait and were drawn to them from their territories. Shy individuals were not usually caught in the traps; bold ones, however, were continually being caught. Once a prairiedog had been trapped and released, he usually became a little cautious about the trap, and especially about the trigger. Some veterans, however, never seemed to learn the trap mechanism; once they began eating the oats, they did not stop even after the trap had closed.

Observation of the reactions of prairiedogs to traps suggests that some of the previously published interpretations of the data from trap records on other kinds of rodents should be modified. First, the absence of new captures and the frequent recapture of marked individuals do not necessarily mean that every animal on the area has been captured (Fitch, 1948). If such a conclusion were drawn from the trap records of prairiedogs, even after a month of constant trapping and with no new captures, there might be as much as a 25 per cent error, because certain individuals avoided the traps entirely. Second, the effect of traps is shown to be a very important factor in modifying the home ranges of the animals. Many individuals were drawn far outside their territories to traps containing bait. Once a trap had been located, frequent trips were made to it, despite the pressure exerted against outsiders by the prairiedogs resident in the invaded territory. Third, the capture of two individuals in one trap does not mean that they were traveling together (Hamilton, 1935; Blair, 1951). Once the position of a trap was learned by the residents, several might go to it independently as soon as they came out of their burrows in the morning. Before the trap had sprung on one individual another often entered, and the two would thus be captured together.

The attempts of a trapped prairiedog to escape were vigorous, especially if the door banged as it closed. In the lever-type trap, in which the door closes quietly, the animals often continued to eat. When they finished eating and found that they could not get out, they seemed to investigate the trap instead of tearing furiously at it. Again, there were individual differences in their reactions to being trapped. Most of them dug at the door and sides. Usually they bit and pulled at the wire. Fierce individuals ran madly against the screen. The electrically welded wires were pulled apart and twisted out of shape at times, and the mechanisms of some traps were ruined by the biting and pulling. Sometimes the prairiedogs injured themselves in their struggles. Teeth were broken off and feet torn until they bled. The most common injury was a skinned nose received when an animal ran its head partly through the wire mesh of the trap. All of these injuries healed without leaving permanent damage to the animals.

The most furious attempt to escape from a trap generally occurred when the observer approached. When I was still at a distance, most individuals would lie down in the trap and remain motionless in an attempt to escape detection. As I drew closer to the trap, the animals got up and dashed about the trap. When I stood directly over an animal, it usually turned its attention to me, striking at me through the wire, snarling, lying on its back, and pawing the air. This defensive attitude might be broken frequently by attempts to escape. Often their defense was so effective that considerable effort was needed in order to take hold of one firmly without being severely bitten. Usually, I waited until one turned its back to me before I clamped my hand on it; it was almost impossible to grasp one of them while it was striking at me. Once in my hand, it wiggled around and tried to bite; it squealed and snarled; its anal glands stuck out, and it defecated or, less often, urinated. When it did get a hold on the glove I wore, it clamped down firmly, closing its eyes and grinding down its incisors without letting loose. Soon, some of its fury subsided, so that I was usually able to mark it while it momentarily held still. A dash to the nearest burrow and a quick plunge down followed its release. Recaptured animals were released from the trap directly without handling. Some of these individuals often ran down a burrow while giving a quick chuckling bark; others ran off uttering a series of calls.

Section Summary

A prairiedog town and its inhabitants form an ecologic community characterized by a particular assemblage of plants and animals, all drawn to the town and dependent upon it to some extent. Forbs, relieved of the competition of the grasses, enter the area and offer food resources to several species of animals. The absence of plants about the burrows attracts the bison to wallow in the exposed earth. The burrows are used by various species of animals as homes and refuges. Finally, the prairiedogs themselves attract parasites and predators which depend upon them for food. The community aspect of the prairiedog town, with its intricate interrelations of the plants and animals, reveals its functional integrity.

TABLE IX

Individual and total numbers of prairiedogs on Ward A, Shirttail Canyon, by age, sex, and year.

Age	Summer, 1948		Summer, 1949		Spring, 1950		Summer, 1950	
	Individuals	Total	Individuals	Total	Individuals	Total	Individuals	Total
Males								
Less than one year .	4, 5, 6, 7, 12, 18^+, 20, 22, 24, 31, 41, 43	12	50, 52, 53	3			Nos. omitted	34
One-year.	. . . .	..	4^x, 6, 12, 20, 24, 41	5	53	1	53	1
Two-year	. . . .	..	. . . . . .	..	6, 24, 41	3	6, 24, 41	3
Two or more years .	. . . .	..	10, 19, 25, 27, 38	5	10, 25	2	25, 37	2
Age unknown. . . .	10, 19, 25, 26, 27, 29, 40, 42	8	. . . . . .	..	. . . .	..	73	1
Invaders.	. . . .	..	. . . . . .	..	37, 73	2	61, 77, 137, 140	4
Total		20		13		8		45
Females								
Less than one year .	1, 3^+, 8, 9, 11, 14, 15, 16, 17, 23	10	. . . . . .	..	. . . .	..	Nos. omitted	23
One-year	. . . .	..	1, 8, 9, 11, 14, 15, 16, 17, 23	9	. . . .	..	. . . . . .	..
Two-year	. . . .	..	. . . . . .	..	1, 8, 9, 11, 15, 16, 17, 23	8	1, 8, 9, 11, 15, 16, 17, 23	8
Two or more years .	. . . .	..	28, 45	2	28, 45, 51, 64, 70	5	28, 45, 51, 64, 70	5
Age unknown	28, 45	2	51, 64, 69, 70	4	. . . . . .	..	. . . . . .	..
Invaders.	. . . .	..	. . . . . .	..	. . . . .	..	141	1
Total		12		15		13		37
Unmarked								
Less than one year ,	13	6		0		0		0
More than one year .		6		0		0		0
Total		12		0		0		0
Grand Total		44		28		21		82

+ Removed by observer.

x Disappeared early in June.

POPULATION DYNAMICS

The aggregation of prairiedogs in discrete colonies offers an excellent opportunity to study population dynamics. The Shirttail Canyon prairiedog town, which contains an estimated 800 inhabitants, is too large for a complete census of the population without more facilities than were available. Consequently, only the population on Ward A was studied. Ward A is somewhat separated from Ward B and the rest of the town by a gentle incline and a few clumps of trees. The population on Ward A was examined from the standpoint of numbers, density, sex and age composition, fertility, replacement, mortality, growth, and migration.

Numbers

The minimum number of prairiedogs living on Ward A at any time in the summer of 1948 was 44 individuals (Table IX). Not all the inhabitants of Ward A were trapped and marked in that year. Observations confirmed the presence of 12 unmarked individuals, and six to eight others were probably present. An estimate of the 1948 population of Ward A would then be approximately 60 individuals. In the summer of 1949 the number of prairiedogs on Ward A was reduced to 28, all but one of which were trapped. The uncaptured individual is believed to have been ♀ 15, which was caught in both 1948 and 1950, but avoided capture in 1949. The next population census was made in the spring of 1950, when 21 individuals were counted, again representing the entire population. When the pups came out of the burrows in the summer of 1950, all or most of them were captured. The number of prairiedogs on Ward A had then increased to 82 individuals. Although 58 pups were captured, it is possible that one or two may have successfully avoided both capture and enumeration by observation. I believe, therefore, that the census of the pups in 1950 is accurate to within one or, at the most, two individuals. There were also five permanent immigrants to the ward in June of 1950.

TABLE X
The number of prairiedogs per acre living on Ward A of Shirttail Canyon for five periods of censusing, July, 1948, to July, 1950.

Time	Area	Population	Density
July, 1948	5.2	44	8.5
July, 1949	5.2	28	5.4
March, 1950	5.2	21	4.0
May, 1950	5.2	78	15.0
July, 1950	7.3	82	11.2
Average	5.6	50	8.8

Density

The number of prairiedogs on the 5.2 acres of Ward A in the summer of 1948 was 8.5 per acre, using the minimum estimated number of prairiedogs for that year (Table X). In the summer of 1949 the area of the ward remained the same, but the density of prairiedogs had decreased to 5.4 per acre. By the spring of 1950 the number of animals had further decreased to 21 individuals, making a density of four individuals per acre. When the pups came from their burrows later in the spring of 1950 and the population on the ward increased to 78 individuals, the density increased to 15 individuals per acre. Shortly after the pups emerged, seven adults of Ward A and five immigrants expanded the area of the ward to the southwest by 2.1 acres. This increased the area of the ward to 7.3 acres and the number of prairiedogs to 82 individuals, with a resulting density of 11.2 prairiedogs per acre. The mean density for the five periods amounts to 8.9 prairiedogs per acre within this ward.

Sex Composition

The sex ratio of the prairiedogs on Ward A varied from year to year (Table XI). The figures for the summer of 1948 are not accurate, because I had not ascertained the sex of all individuals. I believe most unmarked individuals were females. It can be seen from Table XI that the females outnumbered the males among the adults during 1949 and 1950, and that the opposite was true for the young. The reduction of the number of young males was apparently due to a higher emigration and higher mortality rates among them than among the females.

TABLE XI
Sex composition of Ward A, Shirttail Canyon, by age groups of adults and young. Four periods of censusing, July, 1948, to July, 1950.

Time	Adults			Young			Totals		
	♂♂	♀♀	Ratio of ♂:♀	♂♂	♀♀	Ratio ♂:♀	♂♂	♀♀	Ratio ♂:♀
July, 1948	..	..	...	12	10	1.2:1	..	..	...
July, 1949	10	15	0.7:1	3	0	...	13	15	0.9:1
March, 1950	8	13	0.6:1	..	..	...	8	13	0.6:1
July, 1950	10	14	0.7:1	34	23	1.5:1	44	37	1.2:1
Totals	28	42	0.7:1	49	33	1.6:1	65	65	1.0:1

Age Composition

The breeding population apparently is composed of individuals at least two years old. Stockard (1930) suggested that the prairiedogs of the species leucurus did not breed until they were two years old. Observations on C. ludovicianus indicate that this species also does not breed until the second spring after birth; consequently, the size of the effective breeding population is much reduced. The number of females two years old or older was very small in 1949 on Ward A (six at the very most), and only one litter of young was raised. In the same year the greatest single segment of the population was that of yearling females. In the spring of the following year (1950) these same females then constituted the two-year-old age class. When these now sexually mature females were added to the older females, the potential breeding population was considerably increased; in fact, it included every female in the ward. In the summer of 1950 there was an increase in the population. The number of sexually mature females in 1950 was 13, with one failing to breed. Age structure of the population, then, is an important factor in estimating the effective population of prariredogs.

Fertility

The calculation of the number of young per litter necessitates the same reservations about accuracy that were pointed out for the ratios of fertility calculated in 1948 and 1949. Table XII shows that the average litter contains 4.9 young. Actually, there is a wide range of variation in the number of young per litter, but exact counts could not be made because of the rapid mingling of the young shortly after they had emerged from their burrows. In some instances, as many as seven or eight young were observed to emerge from a single burrow. Other litters of known size contained only three or four young. This rather broad variation in the number of young per litter is apparently not due to postnatal mortality. Stockard (1930) found from two to ten embryos in the uteri of leucurus. I found three embryos in the uterus of one female ludovicianus. Another female in captivity gave birth to three young. It seems likely that neonatal mortality is low.

TABLE XII
Fertility of two-year old females in Ward A of Shirttail Canyon 1948-1950.

Year	Two-year Old ♀♀	Breeding ♀♀	Per cent of Two-year-old ♀♀ Giving Birth	Young	Young per Litter
1948	8	5	62	27	5.4
1949	6	1	17	3	3.0
1950	13	12	92	58	4.8
Means	9	6	66	29.3	4.9

Replacement

The replacement of some of the population each year is partly due to reproduction and partly to immigration. In prairiedogs reproduction accounts for the major part of replacement. One measure of replacement[4] is the number of offspring in one generation divided by the number of young in the parental generation. The number of young in the second generation will be affected by the mortality rate of the first generation. Such calculations depend upon a rather long period of observation, and the three years of this study make only one such calculation possible. Of the 22 marked young born on the study area in 1948, only ten were present to replace their generation with approximately 32 young in 1950. The replacement index in this case is, then, 1.5. Later reproduction by the 1948 generation would increase this index. Since the replacement is greater than unity, population growth has occurred. The growth of the population by migration will be treated in a separate section.

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[4] The replacement index used here does not compare the increase or decrease of the actual population in terms of what is expected in a stationary population (Thompson, 1931).

Mortality

Mortality and emigration are the causes of population decline. Since no measure of emigration was made, it will be considered along with mortality. Mortality and emigration have the same effect on any population. Actually, no emigration from Ward A is known to have occurred, for no individuals marked there were ever observed elsewhere in the town. The data on mortality are also incomplete, the death of only one pup being certainly known. The effectiveness of mortality alone or emigration alone in producing a decrease in the numbers of prairiedogs on Ward A is not known; only the combined result of both is measured.

The total effect of mortality and emigration on the study area (Ward A) can be expressed as the percentage of the total population lost during a given period of time. Estimates of mortality in the total population each year can be made by accounting for the percentage of the population lost per year: in 1949, 33 per cent; in 1950, 32 per cent. Similar estimates can be calculated for various segments of the population (Table XIII, XIV, and XV). The calculations in these tables have been made exclusively from the marked individuals on the study area which were recognized in at least one subsequent year.

TABLE XIII

Per cent of each age class of marked animals lost per year on Ward A of Shirttail Canyon.

Age of Marked Animals	1948-1949		1949-1950		Total Loss	Per Cent Loss
	Individual	Loss	Individual	Loss		
Less than one year	3	0	58	1	1	2
One year	22	8	3	2	11	44
Two years	..	..	14	3	3	23
More than two years	..	..	5	3	3	38
Totals	25	8	80	9	18	16

The figures in Table XIII indicate that mortality is particularly high in the first year of life, although not in the very young. Apparently, the young suffer little mortality during their first summer of life, but during the winter and early spring of the following year mortality takes a considerable toll. Perhaps the rigors of the winter environment are directly responsible for many deaths. The animals also are probably exposed to heavy predation in winter. There is much social unrest during the mating season in spring, and social pressure may drive certain individuals away. Individuals which survive their first year of life have almost twice the chance to live another year that they had in their first year.

TABLE XIV
Per cent of loss of marked individuals from year to year on Ward A by sex. Young of 1950 omitted.

Sex	1949			1950			Total		
	Individual	Loss	% Loss	Individual	Loss	% Loss	Individual	Loss	% Loss
Males . . .	19	10	52	13	7	54	32	17	53
Females . .	17	0	0	15	2	13	26	2	8
Totals	30	10	33	28	9	32	58	19	33

There is an indicated difference in mortality between the sexes: young males suffer greater mortality than do females, particularly at the age of one year. This sexual difference in mortality again suggests the possible effects of social factors. The males are much more likely to be forced out of the settled area by dominant males than are the females. Some males are lost from the area through emigration. A young male displaced from his home is undoubtedly more subject to predation and to environmental adversities than is a female which remains in the home territory.

TABLE XV
Per cent of a single generation of marked animals lost each year on Ward A of Shirttail Canyon. Young of 1950 omitted.

	Individuals at Beginning of Year								
	1948 - 1949			1949 - 1950			1948 - 1950		
Generation	Individuals	Loss during year	% Loss during year	Individuals	Loss during year	% Loss during year	Individuals in generation	Total loss during 2 years	% Loss during 2 years
1948	20	6	30	14	2	14	20	8	40

Probably little mortality results directly from combats between males. Combat scars were not observed in the old males, and individuals appeared to be unharmed even after severe combat. That fatal wounds may be inflicted in the course of a battle, however, was suggested in one instance. When we made our camp near a group of burrows, the inhabitants moved a short distance away. Later we released three young prairiedog pets, which took over these burrows next to our camp. The old residents became bolder since we offered them no harm, and they were decoyed closer to camp by the tame pups. One of the pups, a male, began to give territorial calls whenever the adult male resident drew near his old burrows in the camp. Apparently, the pup created a great deal of hostility in the adult male, which chased the pup upon every occasion when we were not on hand to interfere. One day he caught the pup and bit it on the heel. The wound became infected and spread far up its leg. Later flies laid eggs, and maggots swarmed over its leg. The pup remained in the burrow much of the time and grew very thin. By the use of antibiotics and the feeding of concentrated foods, we were able to keep the pup alive, although it is doubtful if he would have lived without our help. One of the other pups disappeared while the old male was around camp; we do not know what happened to it. Such a situation was unnatural, since pups usually have friendly adults nearby to protect them. The incident does show that fatal wounds may be inflicted in battles between prairiedogs.

Mortality, then, plays an important part in controlling the size and composition of the population. Many prairiedogs are lost from the population before they reach breeding age. Males are more numerous at birth, but the sex ratio is generally reversed as the generation matures because of the higher mortality or high emigration rate of the males. Higher mortality rates would be expected among the females as the age of the generation increases. Old prairiedogs may be eliminated from the population by their inability to cope with adverse social or environmental conditions.

Growth

The growth of this prairiedog population is not so conspicuous as its fluctuations in number from 1948 to 1950. From a total of almost 60 prairiedogs in 1948 the population of Ward A declined to 28 individuals in 1949. The population was augmented in 1950 by a large number of offspring, bringing the numbers up to 82. The long interval between the birth of the young and the time when they breed may account for part of the fluctuation in the size of the population. Mortality during the two years before the individuals of each generation breed reduces their numbers considerably in the first year and somewhat less in the second year. If a population is made up largely of individuals of one generation, fluctuations will be inevitable until the age composition becomes equalized, a situation which is characteristic of older populations. The 1948 crop of young was represented in 1952 by at least six females of breeding age. If they and perhaps additional survivors reproduced in 1951 (which seemed apparent, to judge from the large number of yearlings in 1952), the oscillatory nature of the population was replaced by continuous growth. The population on Ward A, then, had reached maturity by 1952 because of the distribution of females throughout all age groups. A growing population can be expected until some check changes the age structure or prevents further growth.

Migration

Migration into Ward A could be effectively measured only when all the residents were known; otherwise, immigrants were confused with unmarked residents. Individuals trapped in other wards and later recaptured in Ward A also served to measure the amount of immigration into the ward. The failure to capture all the residents of Ward A in 1948 made it impossible to estimate the total amount of immigration that occurred between 1948 and 1949. The presence in Ward A of one adult male (No. 38) that had previously been captured in Ward B indicates that some immigration occurred between the summers of 1948 and 1949. The amount of immigration between July, 1949, and July, 1950, is exactly known, since the entire population on Ward A was captured in 1949. Between these dates seven individuals entered and remained in the ward. Two adult males arrived between July, 1949, and February, 1950. One (No. 37) came from Ward B; the other five immigrants arrived in June, 1950, and settled in the area of expansion to the southwest of the old, inhabited parts of the ward. There were four males and one female in this group. Two of the males had been previously trapped in Ward B. The percentage of immigrants in the population on Ward A in July, 1950, was 8.5.

In addition to the immigrants that remained permanently on Ward A, many merely passed through or remained for a few days. Most of these individuals were not captured; therefore, their exact numbers are unknown. They probably had little effect on the population of the ward because of the transitory nature of their visit.

Migration between prairiedog towns and new colonies established in previously unsettled areas was not observed. Reports have been made that towns once exterminated have been reinvaded some time later by prairiedogs that lived no closer than several miles. Osborn and Allan (1949) suggested that a town in Oklahoma was abandoned by prairiedogs which moved to another town a mile away. I have never seen prairiedogs, however, at any distance from a town. In checking for a possible route of travel between the Shirttail Canyon town and the closest one to it, a mile to the east, I could not find any habitat that might serve as a channel for dispersal. Other towns, however, may not be so effectively isolated from each other. A rancher in the Black Hills region told me that he had once seen five or six prairiedogs moving across the prairie in April or sometime in early spring. This observation suggests that migrations may occasionally be made in small groups. If positive information could be secured about the frequency, cause, and method of execution of such migration, it would be of biological importance.

Homing is a type of movement directed toward the homesite rather than away from it. Although natural causes for homing are probably rare in prairiedogs, they may occur in an individual which has wandered in search of a new home and, failing to find one, return to his old place of residence. This might have been the situation with one wanderer (No. 125) that was caught on the area of expansion and was later seen on the floor of the canyon, presumably at the place from which he came. Most reports of homing in rodents (Murie and Murie, 1931; Burt, 1940; Aldous, 1937) are the result of the experimental procedures of releasing an animal some distance from its home and awaiting its return. On two occasions I removed prairiedogs from their home ranges and put them in a strange territory, primarily to observe their behavior. One individual was released within sight of its home. The other was taken about one-fourth of a mile away from its home, which was separated from the point of release by the canyon slopes and scattered trees. The view and also any direct route of return were thus effectively blocked. In both cases the prairiedogs returned to their home ranges. The one released closest to its range returned on the same day. The other was seen back at its point of original capture a week later, although it might have returned earlier. These examples indicate the strong attachment of a prairiedog for its home and suggest that long migrations would be made only under pressure.

Section Summary

The population of prairiedogs on Ward A is not completely isolated; however, if it is analyzed as a unit in which every individual is known, some of its dynamic aspects may be understood. The numbers of prairiedogs in the ward are highly variable, owing largely to changes from time to time in the sex and age composition of the population. The number of females two years old and older in the population determines the size of the yearly crop of offspring. It is likely that the average number of young per litter does not change much from year to year. The number of individuals two years old and older in the population is, in turn, determined in part by their mortality and emigration rates. It was found, for example, that 50 per cent of the 1948 generation remained on Ward A until they were two years old, at which time they could reproduce and replace themselves with their offspring. The length of the reproductive period of female prairiedogs is not known to exceed three years; if their mortality continues at the rate which prevails during their first two years of life, the period is necessarily short, two or three reproductive seasons. The fluctuations in the population size of Ward A can be explained on the basis of the age composition in that area; in any one year the population was composed of breeding two-year-olds and their young or predominantly nonbreeding yearlings. Less extreme fluctuation may be expected on other wards of the Shirttail Canyon town, where the individuals may be more evenly distributed throughout all age groups. Growth of the population is primarily the result of reproduction, although some immigration occurs. Immigration into Ward A may be higher than into other wards more centrally located in the town. Five of the seven immigrants invaded the new area of expansion, which was previously uninhabited. Immigration into wards which lack an adjacent uninhabited area may be less frequent, since immigrants into settled areas are repelled by the residents.

ORGANIZATION OF THE POPULATION

A prairiedog town occupies a geographical area characterized by the presence of burrows and by modifications of the vegetation resulting from the activities of the inhabitants. The prairiedogs which inhabit a town may be called the town population (referring to the inhabitants as a biological unit) or a town society (referring more specifically to the social behavior which unites the inhabitants of the town as a whole). Each prairiedog town is a discrete unit, and most of the activities (except migration) of the inhabitants are conducted within its boundaries. The intervening area between towns is not inhabited by prairiedogs. A large town, such as the Shirttail Canyon town of 75 acres, is often divided into two or more subunits, here called wards, which are more or less separated from each other by topographical or vegetational features over or through which the inhabitants seldom pass. The inhabitants of a ward are called the ward population or ward society, the terms referring respectively to their strictly biological activities or to the social aspects of their organization. The inhabitants of each prairiedog ward are usually divided into two or more social groups, here called coteries. A coterie territory is that part of a prairiedog town which is defended by the members of a coterie.

Town

There were seven prairiedog towns in Wind Cave National Park in 1947, when they were examined and mapped by Mr. Cole. The shortest distance between any two of the towns in the park was one-half mile. These two towns, at the northern boundary of the park, were almost certainly connected at one time, and, unless further human control is exercised, they will probably expand until they are connected again. The other towns in the park are separated from each other by at least a mile of uninhabited land. The town nearest to the Shirttail Canyon town is a mile to the east, separated from it by terrain that is unsuitable for prairiedog occupation.

The size of the prairiedog towns in Wind Cave National Park varies considerably. The town nearest Shirttail Canyon covered about nine acres in 1947, in contrast to the 75 acres covered by the Shirttail Canyon town. Some large towns are not continuous because of interruptions of the terrain or vegetational barriers. Such a town, however, may be considered a single unit if the inhabitants are within sight of one another or have frequent contact. On the other hand, if a town is divided by the terrain or vegetation to such an extent that the nearest inhabitants on each side of the barrier cannot see each other or if they do not readily cross the barrier, each unit is given the rank of town.

Ward

Adjacent wards of a prairiedog town may be isolated from each other to some extent by a difference in the level of the terrain, a hill, a belt of trees, a stream bed, or a road. There is some exchange of animals between the wards of a town, particularly between those wards which are close together. A prairiedog may cross from one ward to another while remaining within sight or audible range of other individuals. Vocalizations are also exchanged between the wards. Generally the fact that there is less movement of prairiedogs between wards than there is within a ward restricts breeding to the ward population. Occasional immigrants from other wards, however, contribute to the breeding population within each ward.

The Shirttail Canyon prairiedog town from 1948 through 1950 was composed of eight wards, separated from one another by the stream bed, a steep slope, or a tongue of forest (Pl. I). Ward A and Ward F, for example, were located on the terrace on opposite sides of the canyon, and their inhabitants were quite independent of each other, except for their vocalizations. On the other hand, Ward A and Ward B were adjacent, separated only be a few scattered trees which grew on a gentle slope between them. The animals of these wards occasionally moved from one ward to the other either temporarily or permanently.

Coterie

Each ward usually contains several of the closed social groups called coteries. The members of each coterie are united in the defense of a common territory against the members of other coteries. On the study area (Ward A), the number of coterie territories varied from four to seven throughout the period of study. Ward B probably contained four or five coterie territories. The boundaries between the coterie territories are well defined, but occasionally they change because of pressure exerted on them by adjacent coteries and by social forces acting within the coterie.

The coterie, as the basic unit of social organization in the town, consists of an integrated social group characterized by frequent friendly social contacts within the coterie and hostile social contacts with members of different coteries. All members of a coterie are familiar with one another and are at liberty to use all of the burrows in the territory. Cohesive behavior, such as grooming, kissing, and playing, is common within the coterie. Displays of antagonism or dominance are rare among the coterie members. In contrast, the social relations between coteries are antagonistic. Members of different coteries fight with each other whenever they meet, and movements between coterie territories are undertaken only at the risk of a combat. All members of a coterie defend their territory against invasions by strange individuals. These patterns of behavior within and between coteries are characteristic of a closed society.

Size of coterie territory. — The size of the coterie territory varies considerably. In Ward A all of the territories were at the edge of the town, and the animals were free to move into adjacent uninhabited regions. Consequently, the size of the coterie territory here is more difficult to ascertain than in regions where the boundaries are more definitely limited on all sides by surrounding territories. In order to estimate the size of the coterie territories on the study area, the mound burrows at their edges in 1949 will be used to define their outer limits. The four coterie territories (named for colors) covered approximately the following parts of an acre: Red, 0.92; Brown, 0.69; Blue, 0.40; and Green, 0.80 (Figs. 6, 7, 8, and 9). These territories were more or less permanent units on the study area. Occasionally, they would split or change somewhat in size, but it is more convenient to describe fluctuations in these basic units rather than to deal with each change as a different territory. In 1949 the adult males of the Blue coterie, for

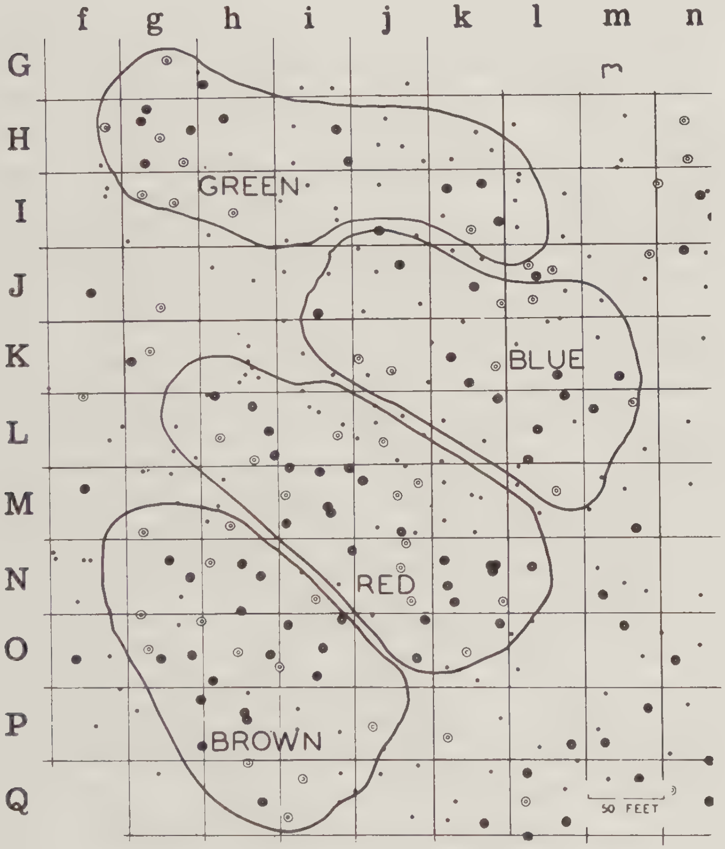

Fig. 6. Position of four coterie territories on Ward A of the Shirttail Canyon town in July, 1948. The boundaries between territories are distinct. Outer boundaries were arbitrarily drawn about the area where the individuals were most active.

example, temporarily divided the coterie territory into two distinct areas covering 0.14 and 0.26 acre, respectively; in the following year, there was no such subdivision, and the Blue territory again consisted of a single unit. Fluctuations in the size of the coterie territories are more extreme at the edge of the town than within the center. The mean area for the four semipermanent coterie territories is 0.70, which is a careful estimate. The territory is also the home range of the coterie

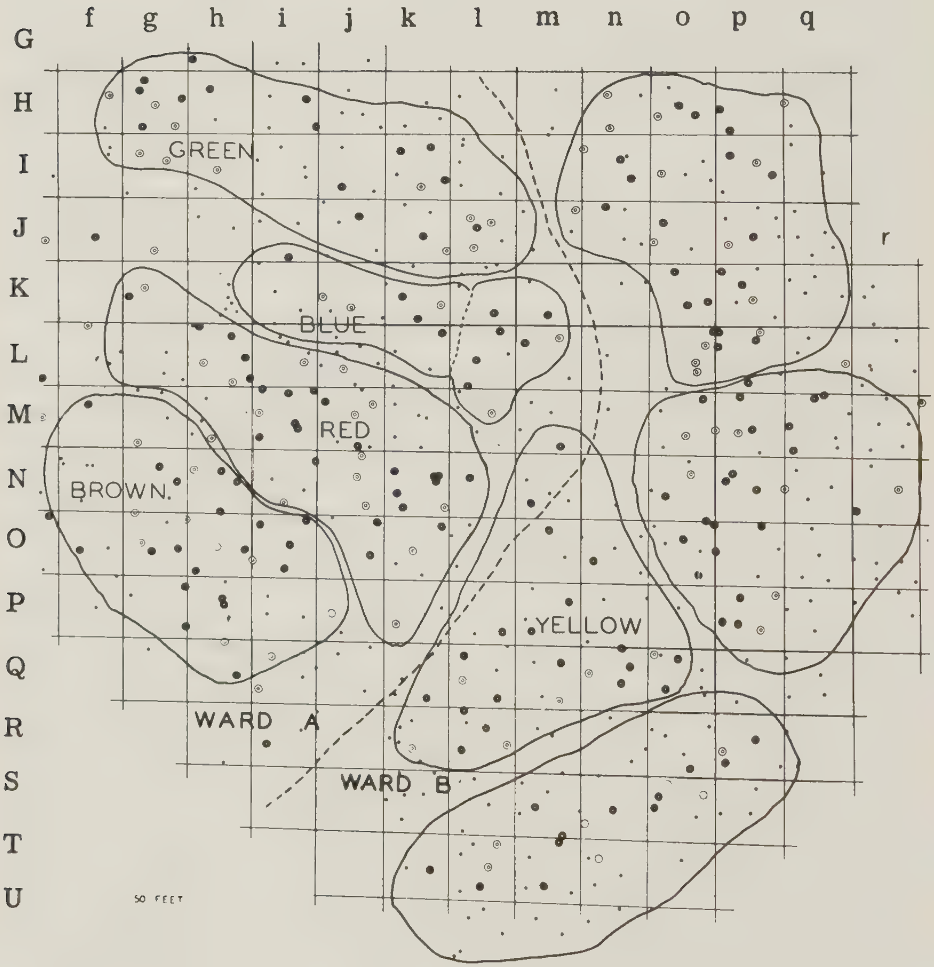

Fig. 7. Position of coterie territories on Wards A and B of the Shirttail Canyon town in July, 1949. The territories in Ward B were not accurately ascertained. The broken line within the Blue territory indicates a separation of the males of the coterie. The females utilized the entire territory.

members inhabiting it. Taken as the home range of each prairiedog, the average area of a coterie territory given above corresponds to an estimate of 0.5 acre by Seton (1929) and 0.6 acre by Soper (1938).

Number of coterie members. — The number of prairiedogs in each coterie varies with births, deaths, migrations, and the re-formation of coteries. Shortly after the young emerge from the burrows, a coterie may contain as many as 39 animals (Red coterie, 1950); however, such a number of individuals is uncommonly large. The population of the

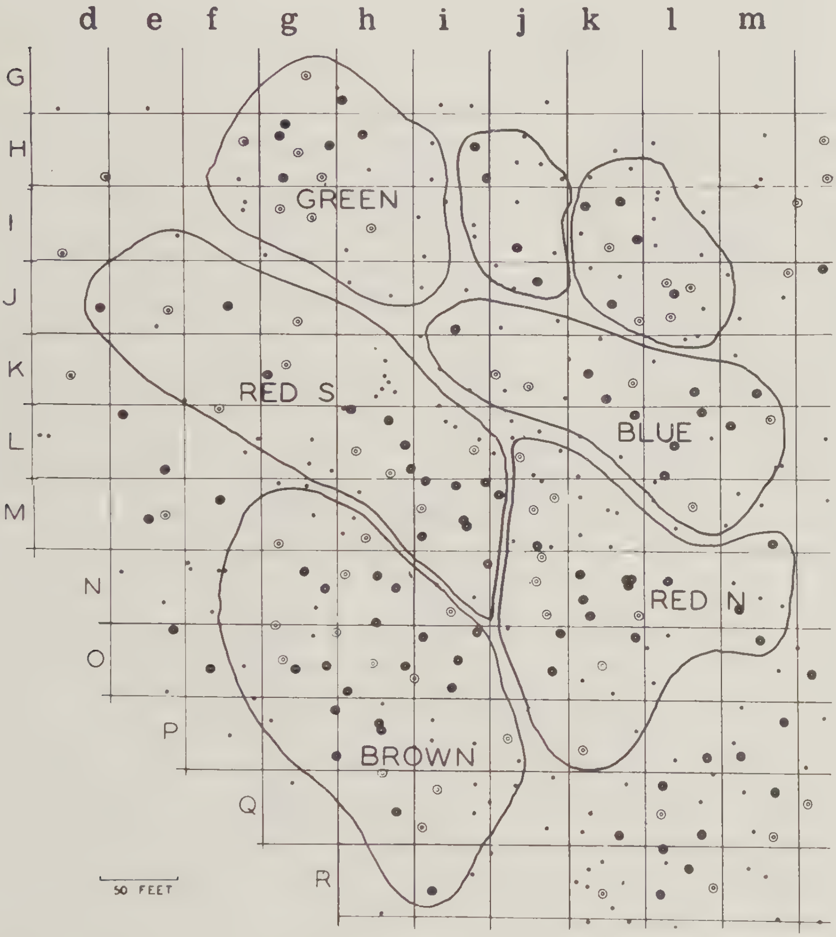

Fig. 8. Position of coterie territories on Ward A of the Shirttail Canyon town in March, 1950. The Red coterie territory was divided during the period of reproduction from February to May. Two coterie territories in the upper right of the map are not given names because of their unstable organization at this time. One was occupied by a yearling male; and the other by a male and a female which failed to reproduce.

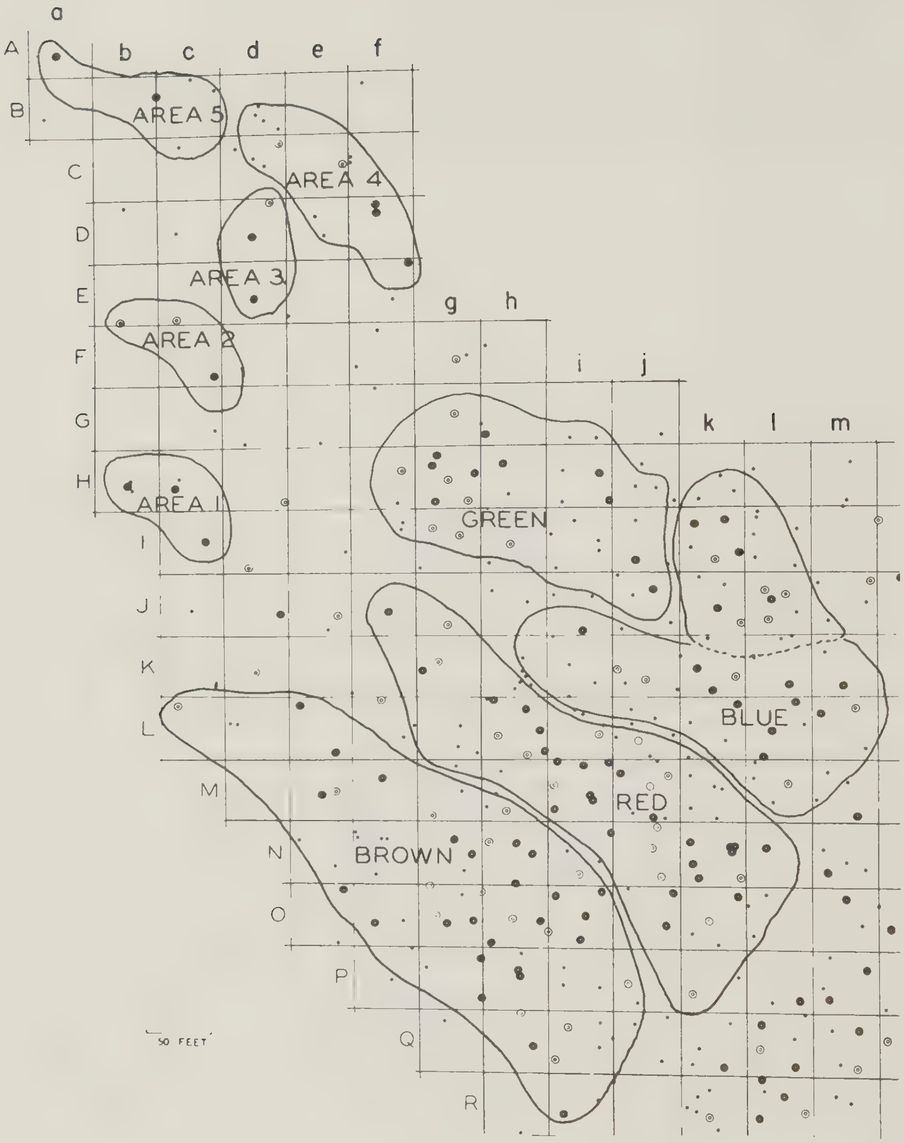

Fig. 9. Position of coterie territories and areas of expansion on Ward A of the Shirttail Canyon town in July, 1950. The numbered areas in the upper part of the map are incipient coterie territories, as explained in the section of the study entitled Expansion of the Town.

Red coterie, which increased from seven to 39 individuals in 1950 as a result of the appearance of the new generation, was reduced again by the departure of the adults shortly after the young came from the burrows. During the mating season division of a coterie often occurs when each adult male in the coterie forms his own social group. The Red coterie, for example, in 1949 contained eight animals, including two males; during the 1950 breeding season it split into two separate coteries, containing three and four animals, respectively, with an adult male in each. In addition to these conspicuous changes in the number of coterie members, mortality accounts for a steady reduction in numbers. Any single figure used to represent the population size of a coterie must be qualified because of the extensive fluctuations in numbers of prairiedogs.

TABLE XVI

Numbers of prairiedogs in each coterie territory (named with colors) of the Shirttail Canyon town during four periods from July, 1948, to August, 1950.

Year	Age	Sex	Red 0.92 acre		Brown 0.69 acre	Blue 0.40 acre		Green 0.80 acre	Mean
1948 July	Adult	♂	2		2	1		3	2
		♀	..		1	0		1	2
	Unmarked	♀	3		2	0		1	
	Immature	♂	3		4	5		0	3
		♀	5		1	4		0	2.5
	Unmarked		6		..	..		..	..
	Total		19		10	10		5	11.0
1949						South	North		
	Adult	♂	2		3	2	2	1	2
		♀	6		4	3	0	2	3
	Immature	♂	0		0	0	0	3	0.6
		♀	0		0	0	0	0	..
	Total		8		7	5	2	6	5.6
1950 Feb. May			North	South					
	Adult	♂	1	1	2	1	2	1	1.3
		♀	2	3	4	2	1	1	2.2
	Total		3	4	6	3	3	2	3.5
1950 June Aug.	Adult	♂	2	..	1	1	2	1	1.4
		♀	5	..	4	2	1	1	2.6
	Immature	♂	16	..	8	6	0	4	6.8
		♀	15	..	6	2	0	0	4.6
	Total		38	..	19	11	3	6	15.4

Table XVI shows the extent of population fluctuation in the totals given for each coterie through the four periods. The mean number of prairiedogs per coterie in Ward A is 8.5, calculated from the total number in each coterie for the four periods (1948, 1949, spring 1950, summer 1950). This figure is much influenced by the new generation of young. By eliminating the young from the calculations, a figure of 4.1 individuals per coterie is obtained, which is a more accurate expression of the size of a breeding coterie.

Composition of the coterie. — The coterie frequently contains a single adult male, two or more adult females, yearlings, and the young of the year. This pattern has many exceptions. Often there are two adult males in a coterie, but one of these is usually dominant over the other, as in the 1949 Red coterie. The presence of more than one male in a coterie may be due to the tolerance of other males by the dominant male, particularly when mating is not in process. There may also be a tendency for the older males to join with each other, with one-year-old males, or with barren females to form a nonreproducing coterie. The northern section of the Blue coterie in 1949, for example, consisted of two old males, which apparently died or were killed during the fall or early winter after they had taken up a more or less solitary life. Similarly, in 1950 part of the Blue coterie included a two-year-old male (in poor physical condition during the mating season), a yearling male, and a barren two-year-old female.

The number of females in each coterie seems to depend primarily on the number surviving to reproduce in the coterie territory where they were born. The number of two-year-old females remaining on a territory to reproduce may vary from one to five. Alien females are usually driven away by both resident males and females, although they may make occasional successful invasions. The number of young in a coterie varies with litter size and with the number of reproducing females. A lack of young in a coterie may result from sexual immaturity of the resident females, the absence of females, or social unrest at the breeding season. Despite variations in the composition of those coteries studied, the general pattern was polygyny. The mean and extreme numbers of each age class and sex composing a prairiedog coterie on Ward A are: adult males, 1.65 (1-3) + adult females, 2.45 (1-6) + immature males, 3.57 (0-17) + immature females, 2.36 (0-15).

Permanence of the coterie. — The coterie territories of Ward A remained essentially the same in size and position throughout the period of study. The most frequent changes of a territory resulted from expansions or contractions of those territorial boundaries which were adjacent to uninhabited areas or to parts of coterie territories which were poorly defended. Other changes occurred when a coterie territory was split as the result of rivalry between two males. Usually such schisms in the territory were later healed without any permanent change in the territory. Boundaries between socially stable coteries were particularly permanent from year to year. The boundary between the Brown and Red coterie territories, for example, did not change throughout the study period. The size and position of the coterie territory is essentially unchanged by a complete population turnover. Males which invade a territory from another ward quickly recognize the boundary which limits their adopted territory. Similarly, pups, which recognize no territories when they first appear above the ground, soon learn the extent of the range. The territory becomes a cultural heritage passed on from generation to generation and from individual to individual. Although individual members of a coterie may change, the social organization of the coterie is to some extent responsible for the permanence of the coterie territories.

An environmental factor which also contributes to the permanence of the territory is the presence of the burrows. The burrows, which are so essential to the life of prairiedogs, are permanent objects in the territory. Many of them are connected underground to form a burrow system. Each system is closely guarded, since the loss of one burrow entrance at the surface may open the entire system to an invader. Consequently, any boundary near an entrance to the system is maintained, and the territory endures as a unit.

Section Summary

The organization of the population of a prairiedog town depends upon the topographical and vegetational characteristics of the town and the social behavior of its inhabitants. Environmental modifications of original vegetation and terrain by the activities of an aggregation of prairiedogs constitute what is known as a prairiedog town. Although the size of the towns varies, each town is identifiable as a unit whenever there is contiguity of its inhabitants and the characteristic environmental modifications made by them. Some towns are divided by topographic or vegetational features into smaller units called wards. Although the inhabitants of different wards (ward population) may communicate with each other and may move across the environmental barriers which separate them, most of their activities are limited to their own wards. A further subdivision of the town population results from the social behavior of the prairiedogs. Within each ward population a group of prairiedogs is united by its cohesive activities and defends a particular section of the ward against all outsiders. The section of a ward defended by a group of prairiedogs is called a coterie territory, and its inhabitants form a coterie. A coterie territory usually covers less than an acre and is utilized by all of its residents. Coteries vary in the number of members, ranging from 2 to 39, with an average of 8.5 individuals per coterie in those which were studied. The effective breeding population of a coterie, not counting the young animals, usually consists of four or five individuals. The sex composition of a breeding coterie generally is one adult male and from one to four adult females. Coteries which are not breeding may have only males, more males than females, or an equal number of each sex. Consanguineous relationships are more likely to occur within a coterie than between coteries. The position of coterie territories in the ward is more or less permanent, although the inhabitants may change as their population turns over and as individuals enter and leave the coterie.

COTERIE INTEGRATION

The prairiedogs that compose a coterie exhibit certain behavioral patterns which integrate them as an organized society. Such a society is distinguished from a mere aggregation of individuals which exhibit no specific responses to their associates. The most important of these behavioral characteristics are discussed under the topics: movements of individuals, group communication and control, co-operation and competition, and social organization.

Movements of Individuals

The movements of a prairiedog within its coterie territory serve to integrate the animal with the environmental features of its home area and with the other members of the coterie. Important features of these movements are: (1) the destination of the individual, (2) the amount of time spent in a particular place, (3) the distance covered by an individual in a day, (4) the manner of movement, and (5) the relation of the movements of one individual to those of another. Movements of an individual may be caused by the search for food, escape from danger, or efforts to guard the territory. The movements may be directed toward or away from social contact. The causes for some movements are not readily ascertained.

Home range. — Most of the movements made by a prairiedog are within its coterie territory. Travels outside the territory are described in a later section. During the period of a single day each individual usually travels over most of its coterie territory, although there is no apparent effort to cover the entire area. Any part of the territory which is not visited on one day may become a center of activity on the next day. Some of the peripheral parts of the territory, however, may be neglected for several consecutive days. The extent of the movements of an individual within its coterie territory is illustrated in Figure 10. It is apparent from this figure that there is little restriction to particular routes of travel, although trips between certain burrows are more frequent than those between others burrows, and certain areas of the territory may form the center of activity on a particular day.

The parts of a coterie territory which are most used may be measured by recording the amount of time each individual spends in different parts of the territory. The 50-foot-square quadrats of the grid pattern on the ward divided the coterie territory into convenient units for ascertaining the position of the individual. Figure 11 shows the amount of time spent in each quadrat by individuals which were observed throughout most of their active day. It can be seen that most of the quadrats within the coterie territory were visited each day by every individual, but that the amount of time spent in each quadrat was not equally distributed. Although each individual was observed for only one entire day, the time spent in each quadrat varies from day to day as ascertained from less detailed observations. Three individuals of the Brown coterie, for example, differed in the amount of time spent in each quadrat, which indicates that no particular part of the coterie territory was utilized more than another part by all of the members of a coterie. Those quadrats at the edge of a ward, however, are utilized slightly more than those towards the middle. This increased use of peripheral quadrats may sometimes indicate a greater abundance of food at the edge of the ward. In the case of ♂ 37, however, those quadrats at the edge where he spent considerable time were vantage points from which he could guard his territory against invaders. The unequal distribution of time spent in the several quadrats clearly shows that the center of activity (Hayne, 1949) need not be in the center of the coterie territory (home range).

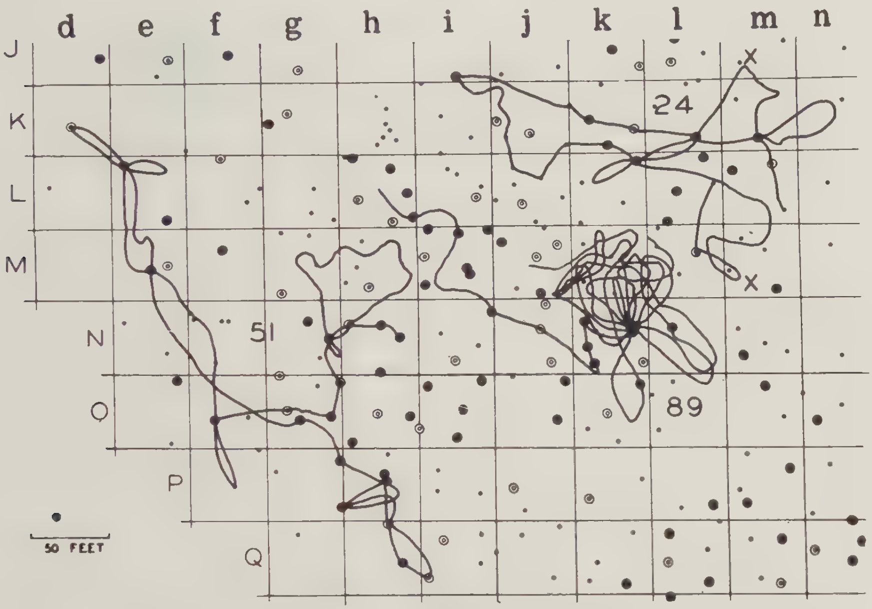

Fig. 10. Movements of three prairiedogs within their respective coterie territories: Movements of adult ♂ 24 of the Blue coterie during 180 minutes of observation on August 15, 1950. He had two disputes (X) with individuals of other coteries at the boundary of his territory. Extensive travels in a small area of immature ♂ 89 of the Red coterie during 430 minutes on August 23, 1950. Extensive movements throughout most of the territory of adult ♀ 51 of the Brown coterie during 286 minutes on July 31, 1950.

Distances traveled. — The distance traveled by each prairiedog during the time that its movements were recorded, as measured from the maps, indicates that the relatively small areas included within a coterie territory do not restrain their activity (Table XVII). Although the measurements of distance traveled daily are crude, they indicate the order of magnitude of the distance covered during the normal activity of a prairiedog within its home range. The mean distance traveled per individual during each day is 5,542 feet, with a range from 3,200 feet to

14,112 feet. Most of the individuals measured covered somewhat less than a mile during each day. There was considerable variation among individuals, however, and also in the day-to-day activity of each individual. The rather extreme distance (14,112 feet) traveled in one day by adult ♂ 37 can be attributed to his activity in guarding the territory on the day he was observed. His coterie had been invaded that day. After chasing out the invader, he was very alert for other attempted invasions. In general, the distances traveled by each individual per day are not very great in themselves, but in relation to the small size of the coterie territory, which usually covers less than an acre, considerable activity occurs.

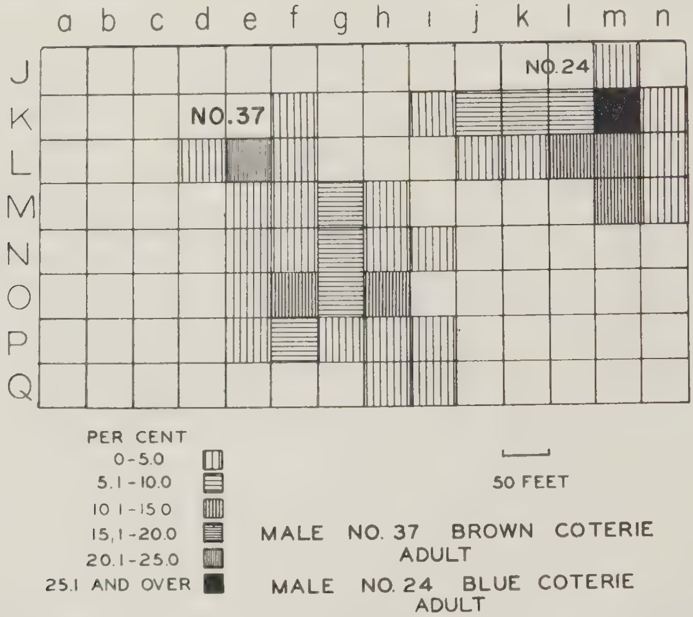

Fig. 11. Percentage of time spent by two prairiedogs in each quadrat within their coterie territories. Adult ♂ 37 of the Brown coterie was observed for 576 minutes on July 19, 1950. He covered almost the entire coterie territory. Adult ♂ 24 of the Blue coterie was observed for 341 minutes on August 15, 1950. He did not spend most of the time in the center of the territory.

The distance actually traveled by each prairiedog is related to the animal's manner of progression. Longer distances are covered when an individual runs from one precise locality to another, such as between burrows, than when it wanders aimlessly over the coterie territory. The fairly uniform distribution of food within each coterie territory enables an individual to feed almost anywhere without going long distances in search of food. The slow progression of the prairiedogs as they move through the vegetation, nibbling food here and there, accounts for only a small part of the distance they cover in a day. Often the dashes between burrows are interrupted when an individual stops to feed for a few minutes; or, conversely, it may suddenly stop its slow ambulations and run to a burrow, sit up, and look around. The distance covered by ♂ 37 was to a great extent due to his running from burrow to burrow within the coterie territory.

TABLE XVII

Distances traveled within the coterie territory by individual prairiedogs observed continuously during one day. Observations made during July and August, 1950, on Ward A of the Shirttail Canyon town.

Number	Sex	Age	Coterie	Feet Traveled	Hours Observed	Feet Per Hour	Feet That Would Be Traveled in a 14-Hour Day
88	♀	3 months	Red	1,976	5.22	378	5,292
89	♂	3 months	Red	1,534	6.68	230	3,220
90	♀	3 months	Red	1,578	6.47	244	3,416
130	♂	3 months	Brown	2,106	6.15	342	4,788
51	♀	2 years	Brown	2,379	9.32	255	3,570
24	♂	2 years	Blue	1,785	5.68	314	4,396
37	♂	3 years	Brown	9,676	9.60	1008	14,112
Means				3,005	7.02	396	5,542

The utilization of the entire coterie territory by each member of the coterie is shown in Table XVIII, which records the burrows visited by each individual of Ward A for a month. These records were collected haphazardly, while other observations were being made. Every time an animal was seen at a burrow, its position was recorded, provided I was not too busy observing other activities, and, since all individuals could not be observed and recorded at the same time and since all could not be observed or identified with equal ease, certain individuals have more records than others. These records, however, are somewhat equivalent to trap records in that they give the exact position occupied by a single individual at one instant. The table shows that the home ranges of several individuals are the same and that each given area is utilized by a group composed of particular individuals, not including others which inhabit adjacent coterie territories. This is the typical coterie structure of a prairiedog town. It can also be seen from Table XVIII that the movements of the individuals of such a social group are almost entirely restricted to their coterie territory. The coterie termed " intermediate" in the table includes individuals which changed their association with individuals of other coteries during the period when the records were kept. The records of ♀ 16 of the Red North coterie show that she was also seen in the Red South coterie territory. Her presence at these burrows in the Red South coterie territory occurred toward the end of the period of observation, when the north and south sections of the Red coterie began to unite again.

Causes of movements. — Many of the movements of prairiedogs are directed toward making social contacts. Two individuals feeding some distance apart may, upon seeing each other, run forward to exchange a kiss. Sometimes, when one individual sees another on a burrow, he runs over to the burrow and sits up beside him. The tendency of pups to follow adults within the coterie territory accounts for some of the distance traveled by pups. Pups also cover much ground in their play activities. Perhaps the greatest distances covered by individuals responding to social stimuli are those resulting from movements concerned with guarding the territory. As was previously mentioned, the extreme distances moved by ♂ 37 were due to this motive. A male which is active in guarding his territory frequently runs to other coterie members to check their identity, and he runs to any part of his territory which may be threatened by an invader. If a dispute occurs between any member of his coterie and an outsider, he usually runs to the scene. At the scene of the dispute, the combatants frequently exhibit great activity as they rush back and forth.

TABLE XVIII

Spot checks on positions of adult prairiedogs at burrows on Ward A, Shirttail Canyon, from May 10 to June 12, 1950. Figures indicate number of times an individual was observed at a given burrow.

Individual Prairiedogs

Burrows	Red North			Burrows	Red South				Burrows	Brown					Burrows	Blue		
	♂25	♀16	♀17		♂6	♀8	♀9	♀64		♂37	♀15	♀23	♀28	♀51		♂24	♀11	♀70
Nk-2	5	17	5	Mi-2	6	10			Oh-2	12	14	4	..	7				
Nk-3	13	26	4	Mi-3	13	14	1	1	Oh-3	2	10	..	..	..				
Nk-5	8	18	6	Mi-5	6	15	2	..	Oh-4	3	..	..	..	..				
Nk-6	25	12	25	Mi-6	5	10	4	..	Pg-1	6	5	..	2	5				
Nk-8	7	11	25	Mi-7	13	8	11	1	Pg-2	25	6	6	2	9				
Nj-1	1	3	1	Lh-1	1	..	7	..	Pg-3	3	1	1	2	1				
Nj-2	..	3	..	Lh-3	9	..	3	9	Og-1	5	2	..	1	2				
Nj-3	6	1	..	Lh-4	6	1	3	4	Og-2	2	4	4	2	4				
Oj-1	9	14	14	Lh-5	11	1	1	10	Og-3	6	2	3	2	3				
Oj-2	..	3	..	Lh-6	15	4	14	..	Og-4	3	1	..	..	5				
Oj-3	6	1	..	Li-4	4	3	14	..										
Mj-1	11	5	7	Mj-4	4	6	..	..										
Mj-6	7	3	3	Ni-4	5	5	1	..										
Ok-4	10	6	10	Kg-1	11	6	2	2										
Pk-1	8	4	1															
Om-2	6	5	6															
Nm-2	9	3	3															
Mm-1	12	5	10															
Mi-3		4																
Lh-6		5	1															
Ni-4		2																
Kg-1		6																

Coteries

Burrows	Brown					Burrows	Blue			Burrows	Intermediate			Burrows	Green	
	♂37	♀15	♀23	♀28	♀51		♂24	♀11	♀70		♂41	♀1	♂53		♀45	♂73
Ng-2	11	2	2	24	8	Lk-4	20	7	12	Ll-4		1		Jk-2	1	
Ph-1	6	2	..	..	15	Kk-1	20	5	12	Kk-6	3			Ik-1	1	
Ph-2	1	1	..	1	2	Kk-3	1	..	..	Kl-1	19			Ik-2	1	
Qh-1	11	5	..	1	5	Kj-1	4	8	2	Ll-5	9	1		Hi-3	4	5
Oi-3	1	1	..	..	..	Kj-3	1	3	1	Km-1	8			Hg-1	1	1
Oi-4	1	1	..	..	..	Ll-1	4	4	1	Lm-2	5	1		Hg-2	21	10
Oi-5	3	5	..	..	1	Ll-2	21	16	1	Jl-5	4	6	16	Hg-5	10	7
Ni-1	1	4	..	..	..	Ll-4	..	1	..	Jl-6		6	15	Hh-1	2	3
Mf-1	5	6	..	9	5	Kk-6	4	1	5	Jk-2		13	21	Hh-2	2	1
Mg-4	1	1	..	2	1	Lj-3	1	2	..	Jk-1		1	8	Ij-2	10	20
Mh-1	2	2	2	..	..	Kl-1	3	2	..	Ik-1	1	7	10	Jj-1	2	2
Qi-1	4	2	1	..	..	Ll-5	2	1	..	Ik-2	1	4	3	Jj-2	1	..
Qi-4	3	2	1	..	1	Km-1	3	..	..							
Of-2	7	5	1	2	9	Lm-2	1	1	1							
Nh-2	12	10	3	..	7	Jl-5	..	..	2							
						Jl-6	..	..	..							
						Jk-2		1	1							
						Jk-1			2							

The causes of some of the movements made by prairiedogs cannot be ascertained, whereas the causes of other are clearly evident. Hunger is probably a prevailing motivation behind many movements, although feeding excursions are usually short. Feeding in the peripheral areas of the town requires trips over greater distances. Similarly, while feeding at a distance from the most used burrows, the animals may have a long distance to run when frightened. Movements caused by the threat of an enemy are directed toward the burrows. Often an individual passes several burrows before running down one, which apparently is preferred to the others. Dashes of over 100 feet are common when a prairiedog runs to the refuge of its burrow. This scurrying to their burrows is frequently seen by an observer who suddenly appears before the animals. It likewise occurs when a bird of prey threatens them.

Group Communication and Control

In this study the term "communication" is employed to mean any expression of behavior which elicits specific patterns of response in other individuals. The most important stimuli to which prairiedogs respond are (1) tactile, (2) olfactory, (3) visual, and (4) vocal. The first three of these means of communication function primarily within the coterie; vocal stimuli, however, affect the relationships of the animals both within and between coteries.

Reactions to tactile stimuli. — Tactile stimulation is important in the recognition of individuals, group cohesion, sexual behavior, play, and fighting. Most of these behavioral patterns employ means of communication other than the tactile sense. Since tactile stimulation depends upon the contact of the individuals concerned, however, it is perhaps the most immediate in bringing about a specific response from each individual.

The "identification kiss" is the most frequent pattern of behavior used to identify individuals of the coterie. The kiss is exchanged whenever two individuals meet; each turns its head and opens its mouth to permit contact with the other (Pl. III, Fig. 1). It is often hastily given when familiar members pass each other in their foraging or when they meet as they run to a burrow together. At times, however, the kiss is prolonged; the animals maintain contact with their mouths and then one proceeds to groom the other. Frequently when two animals meet and kiss, one will roll over on its back, while still maintaining contact with the mouth of the other. Sometimes the kiss ends with both animals stretching out side by side and then moving off to feed with their bodies pressed close together. If two animals of the same coterie meet near the boundary of the territory, or under any other circumstance in which their identity might be questioned, the visual patterns of behavior before the kiss become the primary means of identification. The animals, upon seeing each other, lie down on their bellies, wag their tails, and then slowly creep toward each other, wagging their tails at intervals until contact is established and the kiss given. A pet prairiedog always greeted my approaching hands with his mouth open in preparation for the kiss, which was made at the contact of my hand with his mouth. This performance was always accomplished before further contact with the pet was made.

The open mouth which characterizes the kiss probably serves as a threat rather than an expression of affection. With the mouth open and ready to bite, each individual is aware that the other belongs to the coterie and is ready to defend itself. Despite the threatening appearance made by a prairiedog preparing to kiss, conflicts rarely develop after a kiss because of the intimacy of the animals concerned. At times the kiss does precede playful scuffles.

Tactile stimulation is also an important mechanism in maintaining group cohesion by the intimate contacts established during the grooming process. One member of a coterie frequently grooms another by nibbling and pawing all parts of its body. The nibbling is done by a rapid movement of the jaws while the teeth pass through the fur and touch the skin. The active member of a grooming team moves its head up, on each series of nibbles, and then starts low again and makes another series of nibbles as he moves his head upward. This nibbling is a very effective form of stimulation, giving a tingling sensation to the skin of a human being on whom it is performed. The active member usually crouches over the passive member, which lies down and slowly crawls or rolls over on its back to expose all parts of its body to the stimulation. Usually the grooming is much sought after by the passive member, as is shown shown by its crawling under the muzzle of the individual which does the nibbling. In this manner it attempts to urge the active member to continue grooming after he has lost interest. At other times an individual which is being groomed will move away, seemingly unconcerned with the attention shown it. The grooming is usually of short duration, seldom lasting more than a minute or two, although at times it may continue for as long as ten minutes. In any grooming team the individuals rarely change positions.

All of the individuals in a coterie engage in the grooming process at times. Males groom females and vice versa; adults groom young, and the young groom the adults or each other. The young are particularly responsive to grooming by adults, whom they chase and crawl under in an attempt to induce nibbling. The demands of this type of physical contact were striking in the behavior of a pet, which would nestle up to one's leg and remain perfectly still for as long as an hour while he was being scratched. Even in the prairiedog town, my pets would come up to me and refuse all food, but would accept prolonged scratching; if this was terminated, they would follow me around for more. If leadership were characteristic of prairiedogs, tactile stimulation would probably be the most effective means of procuring followers. Indeed, the pups apparently followed the adults around specifically for the purpose of being groomed. One attempt was made by an adult female to induce a pup to follow her to another burrow after she had failed in her previous efforts to carry the pup there. The female caressed the pup and then ran on a few steps. If the pup failed to follow, the female returned to give the pup another caress and then ran on again. The pup followed her several times, but finally became frightened and ran to a different burrow.

Tactile stimulation is predominant in play and in fighting. Since play is usually in the form of play-fighting, they will be considered together. Actual fighting contact between combatants is usually brief but very intense. Combatants rush at each other and then pounce, clasping with their forepaws, while their teeth inflict the bite. The pair then become disengaged, usually as a result of their tumbles. Once separated, they again withdraw and prepare for another rush, unless one of the combatants retreats, whereupon it is closely pursued by the victor. As the animals rush at each other they often meet in mid-air and are knocked apart by the force of the impact. While standing close to each other, the combatants paw and thrust with their forefeet, which serve to push an opponent away or grasp him to administer a quick bite. Play-fighting is generally much slower, and the combatants may wrestle with each other as they roll around on the ground. A serious conflict usually resembles a bouncing ball rolling across the ground, until the combatants separate and chase each other back and forth.

Other types of tactile stimulation probably occur, but were not observed. Prairiedogs may respond to the warm bodies of their companions inside the burrows at night or in hibernation. The animals frequently rest outside the burrows while they are in physical contact with each other. Primary sexual behavior was not observed, but it is obviously a form of tactile stimulation while the animals are united in copulation.

Reactions to olfactory stimuli. — Olfactory communication is much less easy to detect than other forms of communication, although it may play an important role in governing the behavior of the prairiedogs. The prominent anal scent glands of the prairiedogs emit a strong musky odor, particularly when the animals are fighting or otherwise irritated. The function of this odor at such times is not known unless it may serve to indicate to the aggressor that its opponent is agitated. At other times the odor emitted from the glands may serve to identify the individuals. Smelling the perineum of animals within the coterie, however, is rare except for sexual investigation. Individual recognition seems to be based mostly upon the kiss. Smelling of feces or urine apparently is not employed by coterie residents to locate the presence of strangers in the coterie territory.

The sense of smell was most conspicuously employed during territorial disputes. These disputes generally occurred between members of different coteries, but were also common among the females within a coterie territory when nesting territories were held. The details of the territorial dispute are described in a later section; however, when the animals were engaged in this activity both members of the dispute alternated in smelling the anal glands of the other (Pl. III, Fig. 2).

The pattern of smelling and turning to be smelled frequently lasted for ten of fifteen minutes. Occasionally a fight followed these disputes, but generally they appeared to function more as a bluff.

Reactions to visual stimuli. — Responses to visual stimulation are predominant among the prairiedogs. Practically all other forms of communication include vision, which usually precedes or accompanies tactile, olfactory, and vocal stimulation. For example, individuals must see each other before they approach for kissing. Likewise, the sight of an opponent generally precedes a territorial cry or dispute. For the most part, recognition is established by sight. The appearance of a stranger on the coterie territory draws the attention of the resident animals, and their behavior, as perceived by the stranger, elicits behavioral patterns which further control the responses of the residents. The particular patterns of behavior which are released upon visual perception can be successfully ascertained only by analysis in the laboratory.

The visual perception of other prairiedogs surrounding an individual which is out of its burrow aids in group cohesion. Prairiedogs always seem to be aware of the presence of other individuals about them. It is likely that some "sense of security" is experienced from this awareness. When an animal is out alone, it usually appears much more cautious and alert than when it is surrounded by members of its own coterie. Each individual always appears to be aware of the other animals about him, and many of his movements seem to be oriented toward or away from the other animals.

The identification of other individuals is essential if the coterie is to remain cohesive and exclusive. Members must be distinguished from strangers if the latter are to be kept off the territory. Most recognition is accomplished before the animals make physical contact with each other and without the aid of vocal or olfactory stimulation. The importance of vision in recognition was brought to my attention whenever I saw the dominant male of a coterie rush as much as 150 feet across the territory to chase a stranger away. At first, I thought that perhaps the members of a coterie were recognized by their physical appearance, which would require the memorization of each member. Later, however, it became apparent that behavioral patterns were most effective in recognition. The behavior of an individual when the dominant male of the coterie rushed at it affected the subsequent response of the male. If the challenged animal ran, it was pursued and, if caught, was bitten. On the other hand, if it held its ground, crouched, wagged its tail, and opened its mouth in preparation for a kiss, the would-be pursuer kissed it, or, upon recognizing this behavior as characteristic of a fellow member, even avoided the suspected animal. This behavior of rushing at an animal was common both within a coterie and between coteries. Within a coterie identification was established by the kiss. Between coteries a stranger was soon identified by its tendency to flee, bark, or meet the rush. Often members of two coteries would meet on a disputed area between the coterie territories. On such an occasion, the challenged animal either sat up and barked at the individual which rushed at it, or met the challange by rushing forward. A territorial dispute then began with each animal taking turns rushing at the other and turning around to be smelled in a "pendulum duel," such as is described by Tinbergen (1952). In these disputes the tail was raised and spread as a further visual cue. The response of one combatant in a territorial dispute is primarily determined by its visual perception of the behavior of the other combatant, although tactile, olfactory, and vocal stimuli may predominate in various phases of the dispute.

During a fight, in play, or in pursuit, vision is an important determining factor in the behavior of the animals concerned. The sight of a running individual generally attracted the attention of other animals, which either pursued the runner or sat up and looked about in an attempt to see what induced the individual to run. A running animal served almost as effectively in alerting others as vocalizations did.

Apparently, sight is important in the formation of various subgroupings within a coterie. The young are often drawn to an adult as soon as they see it, particularly if the adult already has a following of young. The male-female subgroup is formed largely by vision, as the male reacts toward the female in response to her behavior.

Tail flicking is a visual cue which probably conveys some message to the animals perceiving it. The tail is most often flicked when an animal is nervous or during an approach of two animals not certain of the identity of each other. Prairiedogs also flick their tails when they are alert to an enemy. Specific responses to tail flicking were not ascertained in the field.

Reactions to vocal stimuli. — The vocalization of the prairiedogs is perhaps one of the most evident characteristics of a town. Prairiedogs utter many different sounds, all of which probably affect the behavior of other individuals in some way. Vocalizations may convey either one specific message or several different messages. Similarly, some vocalizations are quite specific in sound; whereas others have many variations and may be interpreted in different ways by the animals hearing them. The cause and effect relationship of vocal communication is often difficult for the human observer to ascertain, but specific behavioral responses in animals perceiving the sound can be noted. The vocalizations which were recognized are classified as follows: (1) warning bark, (2) hawk warning, (3) defense bark, (4) muffled bark, (5) territorial call, (6) disputing churr, (7) chuckle, (8) fear scream, (9) fighting snarl, and (10) tooth chattering.

The familiar warning bark is one of the most common vocalizations in the town. It consists of a short, nasal yip which varies in intensity and frequency in accordance with the stimulus that produces it. Usually, the first few barks are particularly quick and penetrating; the later barks are less frequent and less intense. The barks are usually too fast to count, although sometimes the prairiedog gives only one bark a second, or even less; an irritated animal, for example, may utter a bark only once or twice a minute while it feeds. While barking, prairiedogs generally sit up or crouch over the entrance to their burrows. The bark is accompanied by a flick of the tail. Prairiedogs may bark for less than a minute, or they may bark steadily for as long as an hour. When an individual is chased into its burrow, it can often be heard barking below. Although barks somewhere in the town are heard throughout the day, some individuals go from day to day without giving the warning bark. The stimulus to provoke it is generally the approach of some possible source of danger, such as a human being, a bison, an antelope, or a coyote. Occasionally an animal barks for no reason that is apparent to the observer. Traps or other unfamiliar objects near their burrows also frequently stimulate prairiedogs to give the warning bark.

The social result of the warning bark is primarily the alerting of other individuals. Upon hearing it most of the individuals interrupt their activities and sit up to see what has caused the alarm. If no danger is apparent or imminent, they continue their activities, regardless of the barking individual. On the other hand, if some possible source of danger is evident, they run to their burrows and they, too, begin to bark. Usually, the prairiedogs pay little attention to barks outside of their own ward, and often ignore those of an individual even in their own coterie territory, particularly if the individual has been barking for some time. This behavior of becoming alert at the first barks, but ignoring subsequent barks if no danger is imminent suggests that the warning bark merely serves to alert other individuals. Before further responses are elicited, the alerted animals must perceive the source of danger themselves.

The hawk warning bark is a more effective stimulus than the ordinary warning bark. This bark differs from the warning bark in that it is faster, more intense, of higher pitch, and of shorter duration. Usually it amounts to no more than five or six quick, high barks, often uttered as the animal is running toward the burrow. It is frequently followed by the warning bark if the object which provoked it is still in the vicinity. More often, however, the hawk or eagle has passed by and the barks cease. In response to this bark prairiedogs do not sit up to perceive the danger themselves, but run immediately, unless the bark is heard from a distance.

Birds of prey most often are the cause of the hawk warning bark, though it may be given at any time when action rather than alertness is required for safety. Whenever I came up the slope onto Ward B without being previously seen by the prairiedogs, this bark would be given. A piece of paper blown from the observation tower would also provoke the bark. Hawks or eagles soaring high about the town or resting in a tree did not provoke the bark, but a low flight over the town or a dive would start the prairiedogs barking and running to their burrows. Birds other than those of prey had little effect on them. The course of an eagle could be traced up and down the canyon by listening to the barks of the prairiedogs as the eagle flew near them. After the eagle had passed, a series of calls (to be described later) were given.

A third type of bark can be detected after one gains some familiarity with the prairiedogs. The defense bark draws attention to an individual who is barking at another prairiedog. This bark is generally given by a female caught at the edge of her coterie territory by a member (usually the dominant male) of an adjacent territory, who by rushing at her tries to drive her back into her own territory. The female, defending her right to be where she is, barks at the aggressive male. The defense bark is slow, often hesitant or interrupted, and high in pitch. Rather than a series of barks, it is a single bark uttered at intervals.

The response elicited by the defense bark is twofold. First, the bark tends to hold off the aggressive male, who paces back and forth in front of the female with his tail spread and his teeth chattering. Second, it often summons the dominant male of the coterie to aid the persecuted female. If the dominant male comes to the rescue of the female, he immediately takes up the dispute with the neighboring male, leaving the female to continue her foraging or to stand back and bark.

The defense bark is also given by the young when the coterie territory is invaded by an adult of an alien coterie during the absence of the resident adults. At first, the young are attracted to the invader, whose treatment of them differs from that of the adults of their own coterie. Consequently, the pups gather around the invader, try to kiss it, or stand back and give the defense bark. If the resident adults are not attracted by the barks, the invader usually leaves of his own accord.

A bark of apparently minor significance can be detected in some disputes. This bark is like the defense bark, but is softer, as if it were muffled or made with the mouth closed. The muffled bark is most often heard in disputes between two females when they are protecting their nesting territories. While one female smells the other, she often utters this bark. It has no effect on the other animals in the coterie, but probably serves as a warning to the opponent in the dispute.

The territorial call is distinctive among the vocalizations of the prairiedogs in that it is executed with a movement of the entire body. In giving this call, the animal throws its body upward and rises on its hind legs with nose pointed straight up and with forefeet thrust out from the body, and then returns to its normal quadrupedal position (Pl. IV, Fig. 1). The vocalization accompanying this pattern is a long call of two syllables. The first syllable is given as the animal throws itself up, and the other follows as it comes down, almost as if the action provokes a deep, vocalized inspiration which is expired as the animal descends. The cry is sometimes executed with such force that the prairiedog leaps off the ground or even falls over backward. At other times, the animal barely gets its forefeet off the ground. This latter behavior is particularly true of the pups which have not learned to give the call with much force and of adults giving a rapid series of calls. Most often the call is given singly or in short series of two or three. It may be given at any time — when the animal is running, standing, feeding, or even when it is part way down a burrow. Many times a prairiedog gives the call immediately upon arrival at a crater.

Many stimuli are known to elicit the territorial call, although all effective stimuli have not yet been discovered. In fact, the call is often uttered when there appears to be no immediate external stimulus. After observing the situations in which this call is given, I find one common element, which may be expressed in the human concepts of security, well-being, and lack of fear. The call is almost the antithesis of the bark, which suggests alarm and fear. Most territorial calls are given in the home coterie territory, where the animal feels secure. An animal may be foraging when it suddenly throws itself back for a call and immediately returns to foraging again. The territorial call is contagious, often passing from one individual to the next within a coterie, ward society, and town society. One seldom hears it given without a response from some other individual.

The call may almost always be expected after a hawk or eagle has passed. At this time the animals again feel safe and utter their calls. Just as the hawk warning bark notifies the others of the presence of a bird of prey, so the territorial calls follow along the canyon immediately after the bird disappears. The call as an "all-is-well" signal may also be given after an animal has been released from a trap or after the door of a nearby trap closes noisily. The sound of the trap closing apparently frightens the animals, but upon perceiving no danger, they respond with the call. On one occasion a prairiedog was observed investigating a rattlesnake which had been staked out on a crater. When the rattlesnake buzzed, the prairiedog ran off a few feet and gave several calls, and then returned to the crater and repeated the performance.

The security experienced by a prairiedog in its own coterie when giving the call conveys a territorial challenge to other individuals in much the same way that the songs of birds do. In anthropomorphic shorthand, the call might say: "This is my territory. I belong here. Nothing can drive me away. Strangers keep out." Animals which are nearby, hearing this proclamation, answer with the same call. This meaning may not be apparent when the call is uttered by the animals peacefully feeding in their own respective coterie territories. But let a prairiedog approach the territory boundary which is guarded by an individual from the adjacent coterie, and the meaning of the call then given becomes clear. On March 16, 1950, for example, the following notes were taken:

> 10:14 a.m. Adult ♂ 6 (Red S) seems to be carefully watching adult ♀ 16 (Red N) from burrow Mj-4 while she forages about burrow Mj-6. 10:19. Male 6 is still watching ♀ 16. 10:20. Male 6 gives territorial call. 10:21. Adult ♂ 25 (Red N) runs to Mj-6, responds to ♂ 6's call, and runs south toward ♂ 6. Male 25 stops while ♂ 6 watches. 10:22. Male 25 moves and ♂ 6 chases after him and then ♂ 25 turns and rushes at ♂ 6. (Dispute continues for 12 minutes.) 10:34. Male 6 goes back

> to Mj-4 and gives territorial call. Male 25 remains at Mj-6 with ♀ 16. 10:35. Male 25 gives territorial call.

On another occasion, the call suggests its threatening nature as ♂ 37 warns ♂ 25 and ♀ 16 away from his coterie territory.

> April 14, 1950. 9:26 a.m. Adult ♂ 37 (Brown) on burrow Ni-1 watching ♀ 16 (Red) and ♂ 25 (Red) come near in Nj quadrat. Male 37 gives territorial call. Then he moves to Oi-4 and gives three calls in response to ♀ 15, which just ran to burrow Oh-3 and gave three calls there. 9:29. Male 37 gives another call and ♂ 25 and ♀ 16 graze farther away into Nj quadrat.

The call may also be given with apparently the same meaning when the status of a coterie member is disputed:

> April 22, 1950. 11:02 a.m. Adult ♀ 8 (Red) chases adult ♂ 6 (Red) at burrow Mj-4 and catches him. They go into a tumbling fight, from which ♂ 6 breaks away and gives a series of territorial calls. Female 8 sits up and watches him.

When ♂ 6 from an adjoining coterie territory was taking over the territory and females of ♂ 37 (Brown), the territorial call seemed to indicate victory, dominance, and challenge:

> March 3, 1950. 2:04 p.m. Adult ♂ 6 (Red) walks back and forth in front of a female of the Brown coterie, with adult ♂ 37 (Brown) between them. Male 37 rushes at ♂ 6 and smells him. They tangle in a fight. Male 6 walks away and gives a territorial call. 2:05. Male 6 sees another female (Brown), runs to her; she crouches. She runs to burrow and ♂ 6 follows her, giving a call on burrow. Male 37 watches.

The territorial call may also be given as a threat:

> June 9, 1950. 10:19 a.m. Adult ♀ 34 (which was invading the Brown coterie) in Pi quadrat. Adult ♀ 37 (Brown) sees her from Ph quadrat and gives territorial call. Female 34 sits up. Both freeze. Male 37 forages toward ♀ 34. This is sham feeding. 10:20. Female 34 goes to Oi-1. Male 37 gives another call, still with eyes on ♀ 34. 10:21. Male 37 runs to Oh-3. 10:22. Male 37 goes to Oi-1 and then chases ♀ 34 into Pj quadrat, at the edge of the Brown coterie.

These few illustrations demonstrate the use of the territorial call in maintaining territories, in challenging rivals, in establishing dominance, and in threatening invaders. The fact that the call is always given by an individual which feels secure in its position seems to account for the spontaneous calls given at intervals while the animals are feeding. The call provokes responses in other individuals if they are safe in their own coterie territories, or it threatens them if they have wandered outside. The call is never given by an invading animal unless he is willing to fight for his position in the strange territory.

A broken churr or snarl is frequently heard among prairiedogs in a dispute. Often the churr is preceded or broken by little barks. Usually, it is made by the persecuted member in a dispute and seems to indicate anger. A male that continues to follow close behind an unreceptive female may provoke her to snarl or churr. A pursued animal most often utters this churring sound while running. My pet would make the sound if I tried to pick him up when he did not want to be bothered.

Fights between prairiedogs are usually silent after the combatants have clinched. When an animal is handled by a man, however, it fights, snarls, screams, and makes a combination of excited sounds too complex to analyze. This vocalization probably has little effect on other prairiedogs, and is directed rather at other species of animals.

Fear screams are particularly characteristic of the young when they are trapped and handled. The scream is a series of cries sounding somewhat like the crying of a human baby. Its effect on other prairiedogs was ascertained from the behavior of a rather tame and bold female (No. 16) in the Red coterie. On several occasions I caught her pups or the pups of a related female. While I held them for marking, they kept screaming. Upon hearing the screams the female came within a foot of me and chattered her teeth. When I released a frightened pup, she came over and tried to carry it back to a burrow. Perhaps if the scream were uttered when a pup was in trouble with a snake or some lesser enemy than a human being, the scream would bring the adults to its rescue.

Tooth chattering, often accompanied by a soft, high-pitched whistle, is a characteristic vocalization of prairiedogs in a dispute. While the animals rush at each other or walk back and forth in front of an opponent, teeth of both individuals may be heard chattering. Occasionally, an individual chatters at some object of which it is not afraid but which it does not like. While I was taking motion pictures at close range, for example, a tame animal chattered her teeth at the camera. The meaning expressed in this vocalization appears to be one of warning and anger. To illustrate its use in a dispute, I quote the following field notes of March 22, 1950:

> 3:19 p.m. Adult ♀ 16 on burrow OK-3, and ♀ 17 approaches, chattering teeth. Female 16 holds her ground, barking softly. Female 17 turns and ♀ 16 smells her anal region, uttering muffled barks. 3:20. Female 6 turns around and ♀ 17 smells her, while chattering her teeth. Female 16 gives muffled barks. Then 16 smells ♀ 17 again, while chattering continues.

Co-operation and Competition

Social co-operation among prairiedogs integrates the coterie by uniting the efforts of two or more individuals toward a common beneficial end. Such behavior may consist of nonconscious aid, which has been termed "proto-cooperation" by Allee (1931). In the co-operative behavior of prairiedogs there is some division of labor, although many activities appear to be similar responses to the same stimulus. Direct competition within the coterie, on the other hand, is not a characteristic type of behavior.

Co-operative activities among prairiedogs occur in vocalizations, environmental modifications, territorial defense, defense of the young, grooming, and play behavior. These co-operative activities, along with some division of labor, aid in integrating the coterie into a functional, discrete unit.

Vocalizations. — The warning barks given as a sign of danger serve to alert other individuals or to send them to their burrows for refuge. Communications which alert other individuals to danger are co-operative to the extent that the bark of one individual may alert another in time for it to escape impending danger. Vocalizations are responded to beyond the coterie territory and consequently unite large parts of the prairiedog town society in this co-operative effort. Although there is a temporary division of labor between the barking individual and those individuals which respond to the bark, no particular individual acts as a permanent sentinel. The bark is given by the first prairiedog which perceives danger.

Home building. — The construction of burrows and the building of nests are most frequently performed singly (although several individuals may work on the same burrow over a period of time), yet two or three prairiedogs were occasionally observed digging and shaping the crater of a burrow at the same time (Pl. IV, Fig. 2). On the occasions when more than one individual worked on a burrow, no division of labor was noted. Each individual acted independently of the other, although their combined efforts resulted in the completion of a burrow or crater. At times one individual may dig out the burrow while another shapes its crater, demonstrating a momentary division of labor. The burrows are constructed by individuals of all ages and both sexes. Other environmental modifications, such as clipping the vegetation, which may result in benefit to all the members of the coterie, are usually made independently.

Territoriality. — Co-operation among the members of the coterie is often important in the defense of their common territory. The territory may be defended against invasion by any member of the coterie, but the dominant male is most active in defense. He is, however, often made aware of an invader's presence by the vocalizations of other coterie members. A frequent pattern of behavior which produces co-operative defense of the territory is as follows: A female or pup becomes aware of a strange prairiedog in the territory and barks at the stranger. This defense bark tends to restrain the activities of the stranger and at the same time draws the dominant male to the scene. He frequently drives away from the conflict the member of his coterie which alerted him before he pursues the stranger or engages it in a territorial dispute. There are many variations of this pattern, some of which may even exclude the presence of the dominant male. The following observations describe in detail instances of co-operative behavior concerned with territorial defense:

> April 14, 1950. At 3:13 p.m., the adult ♂ 6 of the Red S coterie dashes at adult ♀ 16 of the Red N coterie. The female barks at the male, and he chatters his teeth at her. Male 6 walks back and forth in front of ♀ 16 from a distance of 5 feet as she crouches and barks. After a minute of this display, dominant ♂ 25 of the Red N coterie responds to ♀ 16's barking and runs more than 100 feet to the scene of the dispute. Male 25 utters a call and then chases ♀ 16 a short distance away, where she sits and watches the subsequent dispute, barking at intervals. Male 25 then dashes at ♂ 6 and they enter a territorial dispute which lasts for seven minutes and terminates without a victor.

Co-operation of two individuals in maintaining the coterie boundary, with the specialization of the male in defense of the territory, is illustrated below:

> April 10, 1950. Adult ♀ 11 of the Blue coterie runs toward her burrow when she meets adult ♀ 16 of the adjacent Red coterie, who is feeding at the boundary between the territories. Female 11 stops, crouches, and then rushes at ♀ 16. Dominant ♂ 25 of the Red coterie is nearby and upon seeing the dispute comes to aid ♀ 16 chase ♀ 11 farther into her territory. After the male and female of the Red coterie make two dashes at ♀ 11, ♂ 25 turns on ♀ 16 of his coterie and chases her from the dispute. He then resumes his conflict with the female of the Blue coterie until she is back in her own territory.

Young individuals of a coterie frequently unite in their efforts to protect the territory against invasion. This is illustrated by the following observations:

> July 14, 1950. A strange adult is chased from the Brown territory into the Red, where it is discovered by a pup of the Red coterie. The pup barks at the stranger and chases her about while barking. Several other Red pups join in the chase. The stranger stops on a burrow, and the pups take turns running at her, smelling her, and dashing away barking. The stranger remains passive throughout this performance. After three minutes with the pups barking and wheeling around her the stranger runs off into an adjoining territory; where she is pursued by the adults of that coterie.

Co-operation in defending the territory is often necessary, since many coterie members may be too small or may not be sufficiently effective fighters to defend the territory by themselves. The assistance of the dominant male or of other members of the coterie is thus important if the territory is to be defended. The young, or two females, may co-operate to drive an invader away, but most frequently the dominant male is attracted to the conflict and engages in the dispute alone.

Defense of the young by an adult female has already been described (see Communication). The co-operation of the female in protecting the young from enemies may be a more frequent pattern of behavior than observations indicate. It is not known whether other individuals are drawn to the assistance of a coterie member in distress, since the fear screams were uttered only when I handled the animals. My presence apparently inhibited any stimulus which might have elicited co-operative behavior in defense of the young.

Grooming and play. — Grooming behavior requires the co-operation of both members of the grooming pair. The benefit derived from grooming is probably of a sensory nature, although it is also important in maintaining group cohesion (see Group Cohesion).

Play behavior requires the co-operation of all the participants. Play is most often observed in the form of unorganized play-fights and pursuits. Incipient games which are similar to "king of the castle" were commonly observed as one individual defended his position on top of a rock or bison chip against another. Most play is limited to the young individuals, although occasional behavior of the adults could only be interpreted as play. On August 10, 1949, for example, adult ♀ 16 and adult ♂ 25 were observed running beside each other, with ♀ 16 frequently turning about to face ♂ 25 after he gave her a gentle tap on her flank with his forepaw. Besides the benefit derived from the constant social stimulation in play, which probably holds the group together, play also trains the young to fight and gives them exercise.

Competition. — In contrast to the frequent displays of co-operative behavior, there is little evidence of competitive behavior among the members of the same coterie. Direct competition for food, shelter, or social position was rarely observed within the coterie. Competition for food occurred only when a small pile of oats was placed before the prairiedogs. Most often four or five individuals would eat peacefully together, even with their bodies in contact. This was particularly true of the adults. The young occasionally attempted to chase one another from the immediate vicinity of the oats, but the aggressive individual was seldom entirely successful in keeping others away; attempts to drive them away never resulted in a pursuit or fight. Such disputes did not result over natural vegetation, and occasionally one individual took food from another's mouth without any struggle. This almost complete lack of direct competition for food is an important factor in maintaining group cohesion.

The burrows are shared by all coterie members without evidence of competition for them except during the period when the females protect their nesting burrows. As soon as the young emerge from the burrows, all strife within the coterie ceases and the burrows are again utilized by all coterie members. Competition for social position is very subtle when present and is described under social hierarchy.

Social Organization

The social organization within the coterie is based on the social position and cohesion of its members, rather than on a social hierarchy where each individual holds a rank on a scale of dominance. There are a few instances of dominance, particularly between the adult males of the coterie, in which one male subtly displays dominance over the other. The somewhat specialized role of one male in defending the territory against invasion likewise tends to place him in a dominant position over other coterie members. There is also some sexual aggression of the male toward the female during the breeding season. No hierarchy seems to exist among the female members of the coterie. Relationships of the adults with the young clearly show that the adults are dominant, but the young are not strictly controlled and they exercise considerable freedom of activity among the adults. The young individuals vary in their activity, which may indicate future social status. There are, however, no prevailing dominance patterns among them during the first summer of their life. In general, the coterie is a closely knit, co-operative group of individuals which exhibit little or no conflict among themselves and which display patterns of aggression mainly outside of the coterie.

The role of the dominant male in a stable coterie is somewhat specialized in his defense of the territory. Often he is the first individual out of the burrow in the morning and the last to go in at night. During the day he makes frequent trips about the territory, checking the individuals in it to establish their identity. Checking the members may be accomplished by a kiss or by merely running toward a coterie member, which then reacts positively toward him by remaining still or darting down a burrow. Strangers in the territory usually flee when the male rushes up to them. The dominant male makes frequent trips to the edges of the coterie territory where he spends much time guarding against invasion. If a member of the coterie other than the dominant male is engaged in a boundary dispute, the male runs to the scene and often drives the other member away in order to carry out the dispute by himself. Consequently, most territorial disputes are between males of neighboring coteries (Table XIX). These specialized functions of a given male in the coterie indicate his dominance over the other members of the coterie.

Male-male. — In coteries where there is more than one male, one is usually dominant over the other. It is in the relationships between these males that a social hierarchy is most evident. Although the males live peacefully together, sharing the same burrows and even grooming each other, occasional exhibitions of dominance occur. The most common display of dominance between males within a coterie is illustrated by the following type of behavior:

> February 26, 1950. 4:06 p.m. Dominant ♂ 37 comes out of a burrow, barks, and runs to an adjacent burrow. Subdominant ♂ 10 runs to the same burrow from the opposite direction, reaches the burrow first, and runs into it. Male 37 arrives

TABLE XIX

Number of territorial disputes observed on Ward A of Shirttail Canyon between March 4 and June 20, 1950.

		Males							Females											Total for Individual	Total for Sex
		6	25	37	24	41	73	53	8	9	16	17	64	11	70	1	45	15	51		
Males	6	..	12	4	4	..	..	..	..	..	5	2	..	1	..	..	..	1	1	30	
	25		..	2	4	1	..	..	8	..	..	..	..	6	..	..	..	1	1	35	
	37			..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	8	
	24				..	24	3	5	..	1	3	1	..	..	..	6	3	..	..	54	121
	41					..	..	..	..	..	1	..	..	2	2	3	1	..	..	34	
	73						..	..	..	2	..	..	..	3	1	..	..	..	..	9	
	53							..	..	..	..	..	..	1	1	1	2	..	..	10	
Females	8								..	..	4	6	..	1	..	..	..	..	..	19	
	9									..	..	..	..	..	..	1	1	..	..	6	
	16										..	..	..	5	..	..	..	..	..	19	
	17											..	..	3	..	..	..	..	..	12	
	64											..	..	1	..	..	..	..	..	1	
	11													..	..	6	4	..	..	33	35
	70														..	2	..	..	..	6	
	1															..	1	..	..	20	
	45																..	..	..	12	
	15																	..	..	2	
	51																		..	2	
Totals						59								97						312	156

> immediately afterwards and gives a territorial call. Then ♂ 10 comes out of the burrow again. A few minutes later, the same display is repeated at the same burrow; this time ♂ 10 comes out of the burrow and kisses ♂ 37. Soon afterwards, ♂ 37 runs to a female and again returns to ♂ 10 and chases him into the burrow with a few fighting churrs. Male 10 comes out and again smells ♂ 37, who leaves immediately to check on another female. The behavior of ♂ 10 was similar to that of the females at this time of the year; that is, he rushed into the burrow as if being chased there by ♂ 37.

The manner in which dominance is established is indicated in the following observation:

> July 31, 1949. (Shortly after the Blue coterie was adopted by ♂ 24, who had been driven from the Red coterie territory by ♂ 6, ♂ 24 established dominance over ♂ 12 in the Blue coterie.) Male 24 chases ♂ 12 down burrow Lk-4 and begins to fill up the entrance with dirt as he circles the burrow with tail spread. After 12 minutes of such behavior, ♂ 24 moves off to feed and ♂ 12 comes out to utter a territorial call, which is answered by ♂ 24, who then chases ♂ 12 into burrow Lk-4 again. Male 24 continues to chase ♂ 12 into the burrow throughout most of the day whenever ♂ 12 becomes particularly active.

A more subtle display of dominance is indicated in the following observation. In this instance the subdominant male had to make the recognition approach and break the tense, silent challenge of the dominant male:

> July 28, 1949. Adults ♂ 4 and ♂ 6 meet at the edge of the Red coterie territory. They approach each other until about six inches apart, and then both crouch low on their bellies, facing each other. Neither moves for a minute. Then ♂ 4 flicks his tail a few times, without getting a similar response from ♂ 6. Male 4 tries to communicate with ♂ 6 several times by flicking his tail at intervals. Finally ♂ 6 flicks his tail and they both crawl toward each other flicking their tails. Male 4 turns his head to one side and they make a long kiss. After the kiss, both individuals rest on their bellies facing each other until ♂ 4 rises on his forefeet, turns a bit, and pulls up some grass. Male 6 soon follows and they graze together for awhile. The entire meeting takes about three tense minutes.

The display of dominance may even be accompanied by caresses and grooming on the part of the dominant male, as shown in the following observation:

> August 17, 1950. Adult ♂ 6 is feeding about 50 feet from a burrow he had been digging in the area of expansion when he hears territorial calls coming from that burrow. He goes over to the burrow and finds adult ♂ 25 there. They kiss and

> ♂ 6 gives a territorial call, while ♂ 25 begins to stalk away with tail lowered. Male 6 goes over to him and ♂ 25 lies down on his belly. Male 6 smells and nibbles him while ♂ 25 remains motionless. When ♂ 6 stops his nibbling, ♂ 25 crawls a short distance away, but stops again every time ♂ 6 follows. When ♂ 25 crawls a yard from the burrow, under the close guard of ♂ 6, the latter returns to the burrow and gives a call. Male 25 crawls another foot away, and when he finds himself no longer guarded by ♂ 6, he gets up and trots back to a burrow 50 feet away, which he had helped to construct.

Apparently more than one adult male in the coterie is tolerated only when one male is dominant over the other. Although displays of dominance like those described above are repeated from time to time between the males, the subdominant male is generally free to conduct any activity in an unrestrained manner, except possibly during the mating season. At that time, if the subdominant male attempts to pursue the females, he either is driven from the coterie by the dominant male or succeeds in splitting the coterie territory temporarily.

Male-female. — There is no consistent pattern of dominance between the sexes within a coterie. Occasionally, a male will pursue a female or rush at her, but these patterns of behavior are related to the aggressive nature of the male in sexual activities or to his role of guarding the coterie territory. Any consistent pattern of dominance which may be interpreted from such behavior is offset by the females' ability to rebuke the sexual aggression of the male and the females' defense of the nesting territory against invasion by the male. In general, the male takes no aggressive liberties with the females, for the latter readily defend themselves at the first indication of dominance on the part of the male. This immediate defensive reaction of the females to any display of masculine dominance prevents a permanent social hierarchy and likewise contributes to the absence of serious fighting between the sexes. To speak anthropomorphically it seems that each sex respects the rights of the other, and any attempt to usurp those rights by either sex is immediately rebuked by a vocalization of complaint or a few strikes with the forefeet, which end the dispute without establishing dominance.

The characteristic aggressiveness of the male in sexual behavior and the retaliation of the female may be seen from the following observation:

> February 25, 1950. Male 25 follows ♀ 17 all over the Red territory, sometimes running across the entire territory to smell her. The female meets his approach with a kiss. When the male tries to smell her, she crouches keeping her genitals close to the ground, and turns about to face him with open mouth. If he persists in his attempts to smell her, she strikes at him with her forefeet, usually only with one strike, and always with her mouth open.

Shortly after the breeding season, when the females are gestating or lactating, they protect their nest burrow against the males and reverse whatever patterns of dominance were established during the breeding season, as indicated below:

> March 21, 1950. 11:55 a.m., ♀ 16 is taking a sun bath on her nest burrow, but whenever ♂ 25 comes near, she gets up and chases him away, softly chattering her teeth at him. Again, while ♀ 16 washes herself on a burrow adjacent to her nest, ♂ 25 goes to her nest burrow. As soon as ♀ 16 sees him there, she runs over and chases him away, uttering a churring bark. He runs away, giving a shriek, which turns into a territorial call on repeated trials. He then gives two more calls and walks to a nearby burrow, while ♀ 16 chatters her teeth at him from her nest burrow.

Later in the year when the reproductive activities of both sexes have quieted, the equality of the sexes in the social order is re-established, as illustrated in the following observation:

> August 15, 1949. Female 16 goes over to ♂ 6, kisses him, and then proceeds to smell around his mouth as if trying to take a morsel of food from it. This apparently bothers ♂ 6 to the extent that he drubs her several times with his forefeet. Female 16 offers no resistance, but gets up and turns around to let ♂ 6 smell her genitals. She then walks away. In a few minutes ♂ 6 comes over to her and appears to try to atone for his harsh treatment of her by lying down in front of her and rolling about under her nose.

Female-female. — Although most coteries contain more than one female, no pattern of dominance is apparent among them. Females use the same burrow, groom one another, and frequently kiss. They feed peacefully side by side and sometimes aid one another in protecting the coterie territory against invasion. Such amiable relationships, which persist throughout most of the year, undergo a change when the females are gestating and lactating, in March, April, and early May. The burrow selected for the nest and a zone with a radius of approximately 25 feet about the burrow are closely guarded by the female against the male and against other females (Fig. 12). The guarded zone is not clearly defined, and, as a result, females of the same coterie may engage in a tail-raising dispute whenever they meet. Those females which have burrows close together meet each other frequently and consequently have many disputes. As many as three distinct disputes between females with neighboring burrows were counted on one day. As a rule, these disputes never become tumbling fights; usually they end in a draw. The readiness with which the females dispute with each other at this time of the year makes them appear to "enjoy" the quarrel. Occasionally, one female appears more aggressive and goes farther from her burrow for a dispute than do the other females, but the lack of association among the females except in these disputes prohibits any dominance pattern.

These disputes continue with the same frequency until the day the pups come from the burrows. Then, within a week the disputes become less frequent and finally stop altogether. Not only do the disputes end, but the females also begin to visit each other's burrows and resume their amicable relations with each other. This remarkable shift from hostility to friendliness in so short a period appears to be partly due to the fraternization of the pups from different litters. Throughout the rest of the year females never show any attempt to dominate each other.

Adult-young. — There appears to be little difference between the adult males and females in their treatment of the young. Both sexes re-

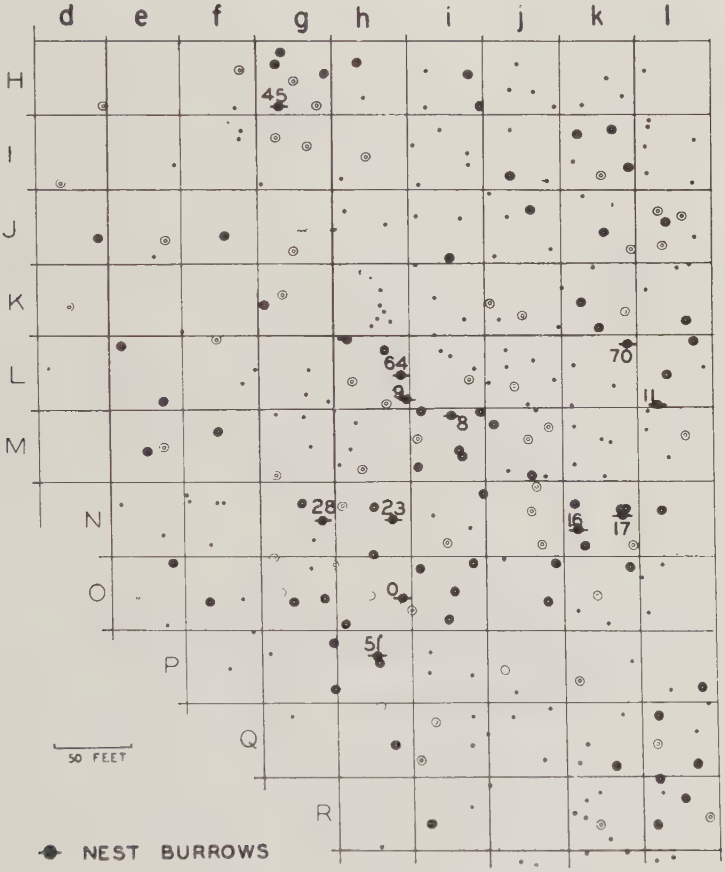

Fig. 12. Position of nest burrows on Ward A of the Shirttail Canyon town during April, 1950. Near the burrows are the identification numbers of the females which raised young in the nests.

act in a friendly manner toward the young during their first summer of life. The adults groom the young and aid them in territorial disputes. The young follow the adults of both sexes about, climb on them, and attempt to play with them just as they play with one another. The pups often persist in their play or in attempts to climb on the adults to such an extent that an adult bothered in this way may drub them a few times with its forefeet to keep them away. On one occasion, subdominant ♂ 25 chased a pup into a burrow and circled the burrow, chattering his teeth and giving territorial calls, while the pup within barked at him. This was an unusual event and was not observed in subsequent relationships between these individuals. Although it is clear that the adults may dominate the young upon occasion, no hierarchy is established among the age groups.

The dominant position of the adults over the young is indicated in the following observations selected to illustrate different patterns of dominance expression:

> June 10, 1950. Dominant ♂ 37 runs to a burrow where a pup awaits him with open mouth. Male 37 stops, the pup approaches him, and they kiss — ♂ 37 keeps his mouth closed. After the kiss, the pup crawls over ♂ 37, who passively ignores him.
>
> June 19, 1950. Male pup 96 pounces on adult ♂ 25, who darts away or braces himself to repulse the charges of the pup. Finally, ♂ 25 runs down a burrow to escape ♂ 96, but when he emerges, he again faces the charges of the playful pup. After three minutes of this attempted play on the part of ♂ 96, ♂ 25 strikes the pup with his forefeet. Male 25 then runs across the territory, but is closely followed by ♂ 96. While running, the adult playfully jumps on the pup until he reaches a burrow and darts down. The pup immediately follows the adult into the burrow.
>
> July 15, 1950. Dominant ♂ 6 returns to his territory and the pups follow him, climbing over him and rolling under his nose. After a few minutes of such attention given him by the pups, ♂ 6 rids himself temporarily of them by striking them with his forefeet. In another minute he is joined by the pups again.

These amicable relationships between the adults and young may change considerably if they meet under strange circumstances. In the area of expansion ♂ 6 was forming a territory in addition to the Red coterie territory he defended. His relations with all of the pups in the Red coterie were friendly. On one occasion a pup from the Red coterie came out to the area of expansion and was received with hostility by ♂ 6, as the following observation illustrates:

> August 17, 1950. Both adult ♂ 6 and young ♀ 88 feed near each other without being aware of each other's presence. As ♂ 6 moves toward ♀ 88 feeding, she sees him and approaches

to kiss him. Male 6 sees her approach and moves toward her. She runs from him, and he chases her about chattering his teeth at her. Soon he returns to feed and she approaches him again. Male 6 lies down and crouches, then pounces on her and bites her before she can escape. When released from the clinch, ♀ 88 runs away fron the vicinity and returns to the Red territory.

Young-young. — Young prairiedogs vary considerably in their activity and size at the end of their first summer of life, but they show no dominance over one another. Aggressive pups do not exert dominance over others in their coterie, but they expend most of their aggression in wandering into adjacent coterie territories or in protecting their own territory against invasion by neighboring pups. By late summer some pups are quite active defenders of the coterie territory. The relations within the coterie, however, are friendly, though not necessarily peaceful. The pups begin to play with one another shortly after they first come from their burrows and continue throughout the summer. The nature of the play evolves somewhat during the summer. At first, the pups wrestle and chase each other around, gently biting each other. Later in the summer, the pups play less, and the play takes the form of pursuits and jumping at one another, more like the fights of adults than like their younger play forms. Wrestling becomes less common since the pups are faster now and seldom clinch. In the mature form of play-fighting one pup does more chasing than the other, which appears to be somewhat persecuted. Actually, the pursued pup is probably not interested in playing at the moment and merely tries to escape the torment of its playmate without a fight. The size of the pups does not affect the play relation, for a smaller individual frequently is more aggressive than a larger one. One runt which was about one-half the weight of its sibs when they emerged from the burrow in the spring remained quite small throughout the summer. This runt developed along with the other pups and was not subdued by its sibs. It received kisses and grooming from the other pups in a manner which indicated that it was as well integrated into the coterie as some of the larger pups. Certainly, it received none of the harsh treatment that Calhoun (1949b) described for the weaker young in a seminatural colony of Norway rats. Three or more pups often played in a free-for-all where no particular one was the "underdog."

Disputes among the pups for oats, which were placed in a small pile, again failed to show that any particular individual was more dominant than the others. If one individual tried to keep the pile to himself by chasing off the others, he was rarely successful; the usual scene at the oat pile was a group of pups crowded around it together, eating as fast as they could. An occasional sharp bark and strike with the forefeet by one pup might temporarily scatter the others, but not for long. Nor did any one individual display more aggressive behavior than another. The frequent fighting among the young for food in the laboratory test situations which were conducted by Anthony (1949, MS) has led him to suspect that social hierarchies are established when the animals are young and prevail through adulthood without further conflict. As tempting as this hypothesis is, it must be further tested because the frequent changes in coterie membership prevent the formation of a stable hierarchy which endures into adulthood.

This apparent equality of the young evidently changes as they approach maturity. Although I cannot describe the development of the relationship in a coterie containing a large number of pups, observations suggest that the young maintain friendly relations as long as they remain together in the coterie territory. Play-fights among the yearlings, however, become more hostile, and it is possible that during such combats some animals prove more aggressive than others. It is unlikely that the aggressive animals remain in the coterie to inherit it from the older dominant male. Rather, they probably leave the coterie of their own accord and attempt to establish themselves elsewhere, or else they are driven out by a vigorous young male from a neighboring coterie. At any rate, only a small number of mature males exist together within one coterie.

Section Summary

Movements by the individuals are an essential factor in the integration of the coterie. All coterie members utilize their entire territory without any threat of conflict among them. Individuals follow no particular paths or routes within the coterie territory, but wander anywhere throughout it (except in newly settled areas where runways between burrows and feeding places can be seen). These meanderings generally take an individual over most of the territory each day. Although the territory is small, movements within it are unrestricted, and an individual may travel a distance almost equivalent to a mile per day. The mean distance traveled by seven individuals, whose movements were recorded, was 5,542 feet, with a range of distance traveled from 3,200 to 14,112 feet per day. Some parts of the territory are utilized more than other parts in any given day, but there is no evidence that strong preferences are made for any particular part. Although feeding is a predominant activity among prairiedogs, the search for food probably accounts for less extensive movements than do social or other stimuli. The pattern of social organization which exists in the prairiedog town controls the daily movements of the prairiedogs by limiting them to their own coterie territories.

Stimuli, whether tactile, olfactory, visual, or vocal, integrate the group either by creating a central source of stimulation, such as a warning bark which causes members of the group to give similar responses, or by synchronizing the behavior of two or more individuals in competitive situations (Carpenter, 1934: 112). Although the communications employed by prairiedogs are rather simple in nature, they are quite varied and include a wide range of sensory stimuli. Many communications are produced by specific stimuli and elicit specific responses. Others are more generalized and serve to communicate only an emotional state which invokes other animals to respond in accordance with the immediate situation. In general, the number, specificity, and complexity of the communications employed by a species serve, to some extent, as an index to the level of social organization achieved by that species. When this index is applied to the prairiedogs, it can be seen that they show a rather high degree of social integration at their phylogenetic level, particularly since the communications are used throughout the entire year and by all age and sex groups.

Co-operation among prairiedogs involves little specialization of function. Most activities are carried out independently, although several individuals may temporarily operate together to carry out a particular activity. Territorial defense, however, is primarily the function of the dominant male of the coterie. Integration within the coterie and, to a lesser extent, within the town population is partly achieved through the co-operation of the individuals in their warning barks, grooming and play activities, and territorial defense.

The weakly established dominance patterns in a prairiedog coterie are congruous with its integrated nature. Although displays of dominance sometimes occur between adult male members of a coterie, social relations among other members are usually friendly and intimate. Disputes within a coterie tend to break the coterie down into separate groups occupying distinct subterritories, rather than to establish scales of dominance within it. The temporary disintegrative effects of social friction become evident in the nesting territories of the females and in the temporary split of some coterie territories during the mating season, when the males establish separate breeding sites. Either the coterie functions as a well-integrated group or it breaks down and is reconstituted.

GROUP COHESION

Group cohesion is well developed among the prairiedogs. As has already been noted, they live together in densely populated towns, which are composed of many smaller social units, the coteries. The organization of the town society into coteries results from friendly behavior among coterie members and antagonistic behavior between individuals of different coteries. Cohesion in the prairiedogs is exhibited in their care of the young, in their social contacts, and in their co-operative activities. During certain times of the year their relationships with one another become less friendly and more hostile. On these occasions group activities diminish and are replaced by more individualistic behavior.

Social Development

Of the early stages in the social development of the young, nothing is known except that siblings live together in the nest under the care of the mother. Probably most young have no contacts with adults other than their mothers while they remain in the nest. Shortly after the young emerge from the burrows they begin to eat solid foods. Weaning occurs at the time when social contacts of the pups increase to include other young and adult animals. The change in family conditions at weaning, with the accompanying expansion of social horizons, "presumably has an influence upon the subsequent readiness to group and upon group behavior" (Schneirla, 1946). Although weaning is necessarily an abrupt change in the parent-offspring relationships, it is not as abrupt in prairiedogs as it is in some other rodents which must prepare for the next litter of young. Even after the young begin to feed independently, mother prairiedogs continue to return to the nest with them at night. Young which have been above ground for a week may still attempt to nurse. When such attempts are made, the behavior of the mother can be observed. She prevents the young from nursing her by caressing them, rolling them over, and grooming their underparts, thus substituting adult behavior rather than rejecting them altogether. Sometimes, the mother remains indifferent and permits the young to suckle without actively repulsing them. Usually, the mother does not remain motionless long enough for the pups to become firmly attached. The intermingling of the young after they first come out of their burrows results in their displacement at night, with the young of one female sometimes spending the night with another female. There are no ill consequences, for one female temporarily adopts the young of another. The equal treatment of the young by all of the coterie adults is also apparent in their behavior above ground. The young of any female in the coterie may attempt to suckle any other female, and the females treat other young as they do their own. The relationships between the male and young are the same as between the females and young of a coterie. Pups even attempt to nurse the male as they nose around his underparts in search of a nipple. The early social relationships among all of the pups in the coterie are similar as they mingle freely with one another in their play. When the pups come out of their burrows in the morning, one of their first activities is to run over to a neighboring burrow and meet the pups coming out of it. This early socialization of the young probably accounts for much of their subsequent social behavior, which binds them together into a social unit.

Dominance

Overt displays of dominance are rare within the coterie. Upon occasions when aggression develops within the coterie, the coterie changes, either through the expulsion of a subdominant member or through a split in the coterie. Aggressive behavior is usually related to reproductive processes, and a partial breakdown of the coterie organization occurs during the breeding season. Direct competition for food under normal circumstances was never observed. Since aggressive tendencies of a coterie member are directed toward members of other coteries rather than toward those of its own, the coterie remains intact.

Social Responsiveness

Coterie members respond to each other in many different ways, such as recognition by a kiss, grooming each other, sleeping together in the same burrow, co-operating in the construction of a burrow, standind side by side on a crater, aiding each other in the defense of the territory, eating and playing together. The frequency with which coterie members are attracted to each other is shown in Table XX. The number of distinct social contacts among the adults of the Red coterie is presented. Observations lasted approximately an hour each day for a total of 19 hours during August, 1949. Probably some contacts between individuals were not observed, because it was impossible to watch all of the eight members at the same time. In a group of eight individuals there are 28 possible pairs of combinations. Each member of the coterie contacted every other member at least once, with the exception of two possible contacts. The absence of two combinations out of a possible 28 is more likely due to incomplete observations than to any actual lack of contact. Relations between ♀ 14 and ♀ 8, and between ♀ 17 and ♀ 9 were the same as between other members of the coterie.

TABLE XX

Frequency of all types of friendly contacts among eight adults of the Red coterie for a total of 19 hours of observation.

	♂ 6	♀ 8	♀ 9	♀ 14	♀ 16	♀ 17	♂ 25	♀ 64	Total
♂ 6	..	2	5	13	17	10	31	3	81
♀ 8		..	1	..	4	1	2	1	11
♀ 9			..	1	3	..	4	1	15
♀ 14				..	8	3	2	5	32
♀ 16					..	13	16	6	67
♀ 17						..	16	8	51
♂ 25							..	4	75
♀ 64								..	28

Total number of contacts 360

Mean number of contacts of each individual 51.4

The nightly grouping of individuals is indicated by the records of the burrows from which they emerge for the first time in the morning (Table XXI). The emergence of individuals from the same burrow in the morning does not necessarily mean that they slept together, but it does indicate a close association with each other, if only at the burrow entrance, where they usually congregate for a few minutes before going off to forage. The data in Table XXII show that several animals may use the same burrow over a period of time. Nightly associations are not restricted to any particular subgroup of the coteries, as is shown in Table XXI. In the 32 mornings that the prairiedogs were checked as they came from the burrows, each member of the coterie was associated with every other member, except for two combinations. Male 24 was never associated with either ♂ 6 or ♂ 25. Ten days after the observations began, ♂ 6 drove ♂ 24 from the coterie territory and thereby made it impossible for ♂ 24 to associate with the other coterie members at night. The largest number of nightly associations were between the two adult males, Nos. 6 and 25. These individuals also shared the greatest number of daytime contacts. All contacts were friendly, but it is possible that the dominant ♂ 6 kept a close watch on the subdominant ♂ 25.

TABLE XXI
Frequency of nocturnal associations of adult prairiedogs of Ward A,
July and August, 1949, as indicated by emergence from
the same burrow. The observations covered a period of 32 nights.

Number of nights associated with

Individual	♂ 6	♀ 8	♀ 9	♀ 14	♀ 16	♀ 17	♂ 25	♀ 64	♂ 24
♂ 6	..	15	16	20	16	20	22	6	..
♀ 8		..	14	11	11	13	10	7	2
♀ 9			..	14	12	13	13	9	2
♀ 14				..	18	15	19	6	1
♀ 16					..	15	18	7	2
♀ 17						..	18	6	1
♂ 25							..	6	..
♀ 64								..	1

TABLE XXII
Frequency of nocturnal use of burrows by the adult prairiedogs of the
Red coterie, Ward A, July and August, 1949. The observations covered a period of 32 nights.

Number of nights in use

Individual	Burrows								
	Nk-6	Nk-8	Nk-5	Nk-7	Mi-3	Ni-4	Lh-6	Mj-1	Nj-1
♂ 6	24	..	2	1	3	..	..	..	..
♀ 8	6	2	..	..	1	..	..	..	..
♀ 9	7	..	..	..	1	..	..	..	..
♀ 14	21	3	1	..	5	..	2	..	..
♀ 16	18	3	..	..	7	1	3	..	..
♀ 17	18	3	1	..	8	..	..	..	1
♂ 24	..	..	..	..	5	..	1	..	..
♂ 25	22	1	2	..	4	..	1	2	..
♀ 64	2	2	..	..	..	..	..	5	1
Total	120	14	6	1	34	1	7	7	2

Stability

Social affinities which arise through frequent contacts between coterie members may be disrupted in an unstable coterie. The lack of stability in the northern section of the Green coterie territory during much of 1950, for example, resulted in frequent conflicts between the resident individuals. It is likely that this social unrest, where strange individuals were going in and out of the coterie territory, was also responsible for the failure of adult ♀ 1 to reproduce. Frequent invasions of the territory by individuals from well-established adjacent coteries prevented the formation of close bonds among resident individuals. Whenever the coterie began to form and exhibit cohesion, it was disrupted by another invasion. The resident individuals apparently had difficulty in distinguishing their friends from their enemies. Consequently, they fought among themselves and joined with members from other coterie territories. Group cohesion was not exhibited in this area of social disturbance as it was in the stable Brown and Red coteries.

Annual Cycle

At certain times of the year the coterie organization of the prairiedog town changes as cohesiveness within the coterie relaxes. Most of these changes are associated with the reproductive cycle and therefore are periodic to some extent. Aside from the reproductive period, which includes breeding, gestation, and lactation, changes in coterie organization apparently follow no annual cycle, with the possible exception of the emigration of adults from the coterie territory after the young have become independent.

The adult males exhibit considerable rivalry during the mating season, which occurs in late February and early March. At this time coteries containing more than one adult male may be split between the males, and smaller coteries and coterie territories may be formed. The Red coterie of Ward A, for example, was split during the 1950 mating season; each part was then composed of one adult male and two or three females. Sometimes an aggressive male succeeds in taking over part of an adjoining coterie territory and thereby enlarges his own, forcing the less aggressive males into nonbreeding coteries. The male in the southern section of the Red coterie, for example, overcame the male of the Brown coterie and temporarily occupied the Brown territory; the male of the Brown was forced into a small area with only occasional access to the females.

After the mating season, during the period of gestation and lactation, the friendly behavior of the females is replaced by antagonism. The females defend their nest territories against invasion by either males or females of their own or alien coteries. Coterie organization is replaced by a number of individual nest territories. Females of the same coterie, however, may associate peacefully with each other and with the coterie male on neutral areas away from their nests. Some females defend their nest territories much more vehemently than do others; some, on the other hand, may even tolerate the presence of the adult male of the coterie near their nest burrows. When the young emerge from the burrows in April, the coteries are again formed as a unified group, and individual territories are no longer defended.

Throughout the year, except during the breeding season, the coterie remains more or less intact. Adults may emigrate in June and July, after the young have become independent of their parents. Emigration of the adults was observed only in the Red coterie of Ward A, although other wards in the Shirttail Canyon town and other towns in Wind Cave National Park also experienced similar emigration of adults. Uninhabited areas adjacent to the old towns throughout the park were invaded by adults in June and July of 1950. The adults often take more than a month to leave their home coterie territory when they are constructing new burrows in the uninhabited regions and are returning at intervals to their old home territory. There is no evidence that the departure of the adults is the result of any antagonism or dominance in the adult-young relationships within the home coterie territory. On the contrary, the adults are welcomed by the pups when they return to the territory. Social contacts between the adults and young, of course, become less frequent as the adults spend more of their time away from the old coterie territory. This peaceful breaking of the social ties between the adult and young members of the coterie changes the membership of the coterie, but has little effect on the coterie territory. Coteries in which the adults remain exhibit the same cohesiveness which previously characterized the coterie. Although adults may migrate at almost any time of the year, June and July are the months of greatest movement.

Changes in coterie membership from year to year indicate that some individuals break their social bonds with the old coterie either by being driven from it or by quietly departing. Intercoterie movements commonly occur in the fall and early winter, as indicated by the presence of new individuals in the study area when I returned in the spring. In February of 1950, for example, the presence of adult ♂ 37 in the Brown coterie and of adult ♂ 73 in the Green coterie showed that they had left their old coteries at some time between September, 1949, and February, 1950. Other individual movements between coteries were observed in July of 1949, when, for example, the yearling ♂ 6 moved from the Blue coterie to the Red coterie. The frequent appearance of strangers on Ward A during the summer months further suggests that the social bonds of any particular coterie member may be broken at almost any time of the year and that migration is not restricted to any particular season.

Section Summary

The social relationships within a coterie are expressed in frequent amicable contacts between the members. As soon as the young leave the nest, they enter a strongly cohesive group of adults which accept them as their own. The young are not abruptly weaned or driven away from their home, but, instead, are nursed by foster mothers and protected against antagonistic individuals from other coteries. Prairiedogs respond readily to social stimuli and make frequent social contacts with all members of the coterie. These contacts occur predominantly in a stable coterie, where individuals can become familiar with one another. Aggression is expressed primarily outside the coterie and is replaced within the coterie by co-operative activities. The seasonal periodicity of the reproductive cycle affects group cohesion by the substitution of individualistic for group behavior. Individuals may break the cohesive bonds and depart from the coterie at almost any time throughout the year.

RELATIONS BETWEEN COTERIES

Relations between coteries are characterized chiefly by antagonism, although some integrative behavior exists through the vocal communications of the prairiedogs. The most frequent cause of conflict is the position of the boundary between adjacent coteries. Other conflicts arise from the attempted invasion of one coterie territory by a member of another coterie. Freedom of movement between coteries is restricted by hostility toward any prairiedog wandering into an alien territory. Occasionally, an unusually aggressive individual is able to invade successfully another coterie territory. The constant threat of invasion keeps the members of each coterie continuously vigilant.

Integrative Activities

Most vocalizations of prairiedogs are audible at a considerable distance, and their effects, therefore, are not restricted to one coterie. Individuals of one coterie may thus be aware of what is occurring in other coteries. Some types of vocalization, such as the territorial call, serve as communication between coteries, whereas others, such as tooth chattering, merely reach other coteries incidentally. Warning barks appear to be independent of coterie organization and may affect indiscriminately the behavior of prairiedogs within as well as between coteries. For the most part, however, those individuals closest to the one barking respond most readily. The warning barks of one coterie may alert the members of another to the presence of a predator and may therefore be a factor in the preservation of their lives. Similarly, territorial calls integrate the coteries to the extent that vocalizations are substituted for conflicts which might arise from attempted invasions into unguarded coteries. Perhaps vocalizations have other functions which are not obvious to the observer. All vocalizations integrate the town society to some extent since they constitute communication between coteries.

Antagonism

The most characteristic social relationship between coteries is one of conflict. These conflicts arise mainly over the position of the boundary between coteries. Here the individuals from adjacent coteries most frequently encounter one another. When an individual, foraging toward the edge of its own coterie territory, passes into the edge of the adjoining territory and is noted by the residents, the first individual of the invaded territory to see the invader rushes at it in an attempt to drive it away. If the invading individual recognizes that it is out of its own territory, it usually retreats. When, however, the invader seems to "feel" that it has crossed no boundary and remains to dispute its "right" to be there, it meets the attack of the defender, and a dispute follows. The typical boundary dispute is a series of bluffing maneuvers, which here are called "tail-spreading disputes." This type of dispute is characteristic of most conflicts between individuals. The individual which rushes at the supposed invader is met with a return rush by the invader, but both individuals stop short of reaching each other in their rushes. Sometimes the distance which separates them at the conclusion of a rush is as much as 25 feet, but more often it is from three to five feet. After they stop and face each other, one of the disputing pair turns, elevates and spreads its tail, exposes its anal glands, and awaits the approach of the other individual, which cautiously draws near and smells the anal region of the exposed individual (Pl. III, Fig. 2). The latter then turns and takes the stance, which allows the former to take its turn at smelling. The disputing individuals alternate with each other in smelling and being smelled until the stalemate is broken by an attempted bite on the rump of one individual or by a gradual return to feeding, with the combatants slowly foraging away from each other. Such disputes usually end in a draw without either individual being defeated.

The tail-spreading dispute over a territorial boundary may occur between any members of the coteries involved. It frequently begins, however, with a female moving onto an adjoining coterie territory, which is protected by the defending male. Although the female herself often disputes her position, her defense barks usually bring the dominant male from her coterie to take up the dispute with the other male. Disputes initiated by the males of adjoining coterie territories are also common, particularly in areas where the boundary is not well established.

The boundary between coterie territories usually is well known to the members, especially where there are active burrows. The underground connection between the larger burrows probably accounts for the distinct boundaries between coteries. If one burrow at the edge of a coterie territory were taken over by an individual from an adjoining territory, it would serve as an opening to the entire burrow system. Consequently, the territorial boundaries near active burrows are distinct and relatively permanent, and few disputes arise about them. In contrast, toward the edge of the town and in areas with few active burrows the territorial boundaries are frequently crossed. Although the boundaries in such regions are not absolutely fixed, they fluctuate within a narrow zone between groups of active burrows. Where coterie territories are changing or new ones are forming, there is much unrest, and disputes between individuals are common. The Green coterie, for example, which was rather unstable in organization, had many disputes with the Blue coterie. On the other hand, disputes between the Brown and Red coteries were much less frequent, except during the mating season and while the pups were learning the territorial limits.

The number of territorial disputes between coteries varies throughout the year. Disputes were most often observed during the spring, when all the animals seem to be particularly irritable. On April 10, 1950, for example, 17 disputes involving members of different coteries were observed in approximately four and a half hours. Of these 17 disputes, 3 were between males of different coteries, 5 between females, and 9 between a male and a female. One half of the total population of the ward, five males and five females, took part in the disputes. All of the disputes occurred at the border between coterie territories. On the same day ten disputes within the coterie were also observed. Most of them resulted from the defense of nest burrows. These disputes included four additional females. Almost three-fourths of the population was involved in one or more disputes. This large number of disputes suggests that the irritability of the individuals may be somewhat contagious. During the summer the number of disputes usually decreases, and many days may pass without a single conflict between the coteries.

Invasions

Boundary disputes usually begin spontaneously when a territorial boundary is accidentally crossed or when an individual from one coterie forages into a disputed area between coterie territories. On the other hand, when an invasion is attempted, the resulting conflict varies according to the motive for the invasion. The motivation of an invading individual may be (1) exploration, (2) a specific food supply, (3) a new homesite, (4) a larger territory, or (5) mates.

An invasion which is motivated by exploration commonly occurs when a neighboring territory is temporarily left unguarded by its members. In the early morning, before the members of a coterie have come out of their burrows or before they have reappeared after being frightened down their burrows, an individual from an adjacent coterie may often explore the unguarded territory. The invader runs from burrow to burrow, putting its head into each, but seldom going down farther. It makes the rounds of the burrows in a confident manner, occasionally giving territorial calls. Upon the appearance of the residents of the invaded coterie territory, the invader returns hurriedly to its own territory or is chased back by the first resident which makes its appearance. Similar explorations may be made when an invader finds that it has crossed a territorial boundary without attracting the attention of the residents. Finding itself in an unguarded territory, the invader may begin to explore those burrows which have been left unguarded. The invader is cautious and alert. Even if a resident individual approaches, unaware of the invader, the latter usually hurries back to its territory. Without other motivation exploring individuals probably do not wander far from their own coterie territory.

Exploratory wanderings sometimes bring reward in the discovery of a food supply, such as bait placed around traps. Once the bait has been discovered in a neighboring coterie, invasions into that territory are frequent, as is verified by observation and by trap records. The caution and alertness of an exploring individual are exercised by an invader attempting to reach such a food supply. The residents in an area being trapped often avoid the traps and may allow less wary individuals from adjacent coteries to reach the traps without interference. If, however, a threat should be made by any resident of the coterie territory, the invader hurries home, often pursued by a resident. An animal trapped in a coterie territory other than its own is harassed by the residents when it is discovered. As many as three resident individuals will gather about a trap which holds an invader, charge at him, chatter their teeth, and spread and raise their tails, while the captured individual tried to escape or to fight back through the wires of the trap. When trapped animals are released in a strange coterie territory, they often run back to their own territory rather than take refuge in the first burrow they come to. In such situations the fear of the strange coterie is stronger than the fear of a human being.

Invasions which are motivated by the search for a new homesite are usually characterized by a more tenacious type of behavior. The invader is cautious and on the watch for the residents of the coterie territory, but is less easily driven away when discovered. The search of an invading individual for a new homesite is illustrated by the following observation:

> June 23, 1950, 5:59 a.m. Adult ♀ 34, who is invading the Brown coterie territory from Ward B in search of a new homesite, is chased back into Ward B by adult ♂ 37 of the Brown. As soon as ♂ 37 returns again to his territory, ♀ 34 forages back to the edge of the Brown coterie territory. Nine minutes later, ♀ 34 barks at ♂ 37. At 6:15 a.m., ♂ 37 chases ♀ 34 in circles around the edge of the Brown territory, but she refuses to leave the area. Female 34 finally dashes down a burrow, and ♂ 37 circles the burrow with tail spread and teeth chattering. She barks from below. Two minutes later, ♂ 37 leaves and ♀ 34 comes out, barks at him, and then proceeds to forage about her refuge burrow, while ♂ 34 watches from a distance of 65 feet. (Although ♀ 34 temporarily held her position in the Brown coterie territory, she later left it and found a new coterie territory elsewhere in the town.)

When a coterie territory is invaded for the purpose of attempting to settle there, the invader usually selects a place which is unguarded. It then proceeds to acquaint itself with the burrows and quietly makes itself at home, but is always on the lookout for the residents. When discovered, it behaves much as ♀ 34 did in the observation given above, that is, it runs around the burrows it has explored, retreats into one when closely pursued, and defends its " right" to be there. Despite the reluctance of such an invader to leave its adopted home, invasions into well-established coteries are rarely successful. Even if an invader succeeds in making friendly contacts with the dominant male, the antagonism of the other coterie members usually suffices to drive it away. Often two or three coterie members unite to drive off the invader.

A coterie most often expands at the expense of an adjoining one which is unstable or which has some territory which is seldom used by its residents. Invasions made for the purpose of expansion are characterized by behavior similar to that of a single individual searching for a new homesite, that is, the invaders display much resistance toward the defenders in an attempt to remain within the invaded region. There is this difference, however, that an expansion of coterie territory is attempted from a resident territory, from which frequent excursions are made by many individuals. This results in a constant pressure on the invaded coterie territory, and unless the residents guard the area well, they lose it to the invaders. Successful expansion generally occurs in areas left unguarded by the residents for long periods of time. Control of the region around quadrat M-m thus frequently changed from one coterie to another as a result of such invasions. This region had little vegetation and was more or less an extended appendage of the Yellow coterie territory from Ward B, whose members guarded it diligently during some periods and rarely visited it at other times. Consequently, it was taken over from time to time by members of the Red or the Blue coteries. Similarly, areas in the Green and Blue coterie territories were frequently exchanged after many disputes and invasions.

The aggressive behavior of an adult male when he is attempting to secure mates or to take over a coterie is another cause of invasion. Males protect their territories by the bluffing maneuvers of the tail-spreading dispute and by a display of antagonism, without coming into direct combat. Old and/or weak males are able to protect their territories in this manner until threatened by another male which is willing to fight for the coterie territory. A serious challenge by the invading male results in a series of combats with the occasional victory of the invader. In such combats there is usually no decisive battle, nor does a change in the males of a coterie occur in a short time. Usually, the invading male dwells about the outskirts of the coterie territory he is trying to enter or makes frequent invasions from a neighboring coterie. At intervals, he enters the coterie territory, tries to associate with the females, and runs around to the various burrows until he comes in contact with the dominant male of the coterie. Then the invader is pursued about the coterie by the dominant male until he is finally driven off. Sometimes the invader may rush into a burrow and protect it against the other male. Sooner or later, however, the males get into a fight, which is interrupted by many pursuits. After several days of this activity, the invader becomes familiar with the area, with the females, and with the combative qualities of the male, and he begins to show more resistance. Finally, the invader may succeed in winning part of the territory and may go on to conquer more, until the resident male is forced entirely out of the coterie territory or into a small corner of it.

Successful invasions of coterie territories by aggressive males are apparently not uncommon. These invasions may occur at any time during the year. One invasion was observed during the breeding season in February, another was observed in July, and others occurred in the fall and early winter between observation periods. Such changes in the dominant males of the coteries are not always permanent. Adult ♂ 6 of the Red coterie, for instance, took over most of the Brown territory for a week during the breeding season of 1950 and afterwards again limited himself to the Red territory. Probably many other unmarked males unsuccessfully attempted to invade a coterie territory. The behavior of a male which had recently move into an uninhabited region at the edge of the town and which made an unsuccessful attempt to invade the Green coterie territory is described below:

> June 6, 1950. 11:39 a.m. Adult ♂ 73 comes out of a burrow and sees a strange male nearby. They meet and immediately begin a fierce fight until the defender (♂ 73) is chased back to his burrow. In a later combat ♂ 73 chases the invader about the territory in circles. This fast pursuit lasts for two minutes. Occasionally ♀ 45 of the Green coterie joins in the pursuit to help ♂ 73 chase the invader out, but her spurts are short. After much circling about the coterie territory, the invader finally heads out toward the uninhabited area, with ♂ 73 close behind him. (The invader was ♂ 140, which was later trapped and marked in the area of expansion where he had established himself. He occasionally made other attempts to invade the Green territory, usually in the absence of ♂ 73.)

Most social relations between coteries are individual affairs and do not involve the united efforts of an entire coterie. A dispute may be initiated by an individual from each of two adjacent coteries and then may be continued by the dominant male of each coterie. In such instances, the females or young which initiated the dispute allow the males to carry it on, or they may stand off and bark at the invader while the male continues the dispute. Occasionally, two members of a coterie unite to drive out an invader or two or more individuals together invade a coterie territory, from which they are chased out by one of the residents. When I was retrapping the Brown coterie in an effort to catch the few remaining unmarked pups, the pups of the Red coterie were attracted to the traps placed close to their territory. Many of them frequently invaded the Brown territory to reach the bait around the traps. This large-scale invasion of the Brown coterie territory drew the attention of ♂ 37 from time to time; he would run at the pups and drive them out. Under such circumstances, ♂ 37 usually chose one individual to chase and pressed it hard, making it snarl and bark. This commotion sent the other young invaders home; however, they soon returned to the traps after ♂ 37 moved off into another part of his territory.

The constant pressure exerted on coteries by invaders necessitates the vigilance of all the residents. The members of a coterie are always on the alert for invaders, carefully watching members of other coteries as they approach the boundary. The dominant male of the coterie is particularly vigilant, running about the territory to check on the identity of the individuals in the coterie, sitting up on special craters or rocks from which he can view the territorial boundaries, and watching the movements of any individual from another coterie which may attempt an invasion. This constant alertness of the prairiedogs has often incorrectly been interpreted as a guard against predatory species; instead, its social function is to watch the threatening activities of other prairiedogs.

Section Summary

The discrete character of the coterie as a social unit is maintained by the defensive activities of its members against invasion and by their inability to wander beyond the territorial limits without conflict. This forceful limitation of the coterie members to their own territory creates social pressure within the coterie, which is released by the outward movements of its members when the defense of an adjacent coterie is relaxed or when the motivation of an individual to move out overcomes the fear of conflict. The usual result of an attempt to invade an adjacent territory is a dispute with members of the invaded coterie and the return of the vagrant. Successful invasions occasionally are completed after many battles, and the invader becomes a member of a new coterie. The social stresses between coteries at the edges of their territories are often punctuated by boundary disputes. Each coterie is on guard against invasion; at the same time its members are ready to invade another coterie territory when opportunity offers.

EXPANSION OF THE TOWN

One reason for the selection of Ward A for this study was its situation at the edge of the town near the only area available for expansion which was not bounded by some physical barrier. Adjacent to Ward A an area of suitable habitat larger than the entire occupied town was available for settlement. I had anticipated learning the relationships between the expansion of the town, its population size, the condition of the biotic environment, and the social behavior of the prairiedogs. Such anticipations were not fully realized because of the complexity of these relationships. Some interesting data were gathered, however, which may throw light upon the causes and the effects of the expansion of a prairiedog town.

History

The area into which the town expanded lies on the terrace to the south and west of Ward A and covers 2.1 acres (Fig. 9). It is entirely covered with grasses (brome, grama, and buffalo grass) which stand about 8-12 inches high in the summer. There is one limestone outcrop where the vegetation is much shorter and where a few rocks appear above the surface. There were three old unused burrows tunneling beneath these rocks. Other small unused burrows were scattered in the tall grass closer to the town. These burrows were without craters and probably were no more than a foot long. Prairiedogs were never seen in this area during the summers of 1948 and 1949. In the summer of 1950, however, they occupied it.

The first prairiedog activity in the area of expansion was observed in the early spring of 1950. At this time the dead grass of the preceding summer was lying flat on the surface of the ground. Prairiedogs could be seen 100-200 feet beyond the edge of their town, feeding on the fresh shoots of grass which were coming up. Tracks in the snow also indicated that prairiedogs had made extended trips to the south of the town. Later in the spring some of the old burrows were enlarged, and new burrows were dug. Some animals remained in the expanded area during much of the day. These activities, which were confined to an area within 200 feet of the town, continued throughout May and into June of 1950. The young of the year along with the adults made use of the new areas.

About the first of June prairiedogs were seen around the limestone outcrop, which was 300 feet from the nearest settled part of the town. From time to time prairiedogs could be seen out on the flat as far as 600-800 feet west of the town. These individuals were unmarked and probably came from parts of the town other than Ward A. It is likely that they came up over the forested slope from the canyon floor north of the area of expansion. There seemed to be a rapid turnover of individuals in this region; some were trapped but were not seen again; other trapped individuals remained. At the same time certain prairiedogs from Ward A began to settle the limestone outcrop by digging burrows farther to the south of the town. By late July most of the prairiedogs which had invaded the area of expansion remained, and further immigration into the area ceased. The Ward A pups which first went into the new area were later excluded from it. No important changes occurred in the number of prairiedogs in the area occupied throughout August, when the expansion for the year came to an end.

Similar expansions of prairiedog towns were seen about Wind Cave National Park in midsummer of 1950. Prairiedogs crossed the stream bed in the floor of Shirttail Canyon and moved down the canyon as far as 800 feet beyond the last burrow at the former edge of the town.

In May of 1952 the area of expansion had increased in size, particularly in the flat lying to the west of the town, which had been occupied only temporarily in 1950. The increase in size, however, was not so conspicuous as were the consolidations of the prairiedogs' holdings obtained in 1950. The entire area could hardly be distinguished from the old parts of Ward A, since burrows were scattered throughout it and since most of the original vegetation had been replaced by forbs.

Causes of Expansion

Population density. — An increase of the population on Ward A in the spring of 1948 apparently did not affect the area of the ward. At that time at least 30 pups were added to the adult population of approximately 20 individuals. Although some expansion of the ward may have occurred between the time when the pups came out of their burrows in May and the time when the first observations were made in early July, there was no evidence of such expansion. All of the burrows appeared to have been well used, and the forbs about them indicated that they had been made at least one year before. Use of the vegetation at the outer edges of the ward might have caused a slight expansion of 15-25 feet, but there was nothing comparable to the expansion of 1950.

The population of Ward A had decreased by July of 1949 to 28 animals. Again, there was no noticeable change in the boundaries of the ward, although prairiedog activity at the periphery continued to clear it gradually of the tall grasses for 10-15 feet back from the edge of the ward. The boundaries of the ward, however, were virtually unchanged.

When observations were resumed in February of 1950, the population was further reduced to only 21 animals. Despite this reduction some prairiedogs on Ward A were observed feeding and digging as much as 200 feet to the south of the ward. Activities in this new region to the south continued throughout the summer and were increased as the pups went into this area, in which there were now scattered burrows. The population reached a maximum of 81 animals when the young were born in April; however, one adult disappeared. Shortly after the pups appeared above the ground, seven of the 20 adults moved still farther south and west on the grassy flat, dwelling in burrows as much as 500 feet from the burrows they had formerly occupied. These seven animals were adults of the Red coterie which, with the addition of the pups, had increased in number more than had the other coteries on Ward A. The Brown coterie, which also increased in number, extended its territorial limits south about 100-150 feet, but did not entirely break away from the old coterie territory, as the adult members of the Red coterie did. By August, 1950, five members of the Red coterie no longer returned to their old coterie territory, completely severing themselves from their young. Two adults of the Red coterie, however, made frequent trips back to the old territory.

These observations indicate that population density is not directly correlated with the size of the town. First, the increase in population density in 1948 failed to increase the area occupied that year. Second, a decrease in the density of prairiedogs in 1949 did not reduce the size of the ward. Third, the initial expansion of Ward A in 1950 occurred before the young of that year were added to the population.

Continued expansion of the ward after the pups came from their burrows suggests, however, that the increase in population had some effect on the emigration of a few adults. Likewise, the increase of the Brown coterie territory to the south after the arrival of the young further indicates that population pressure may be a factor causing expansion. The Blue and Green coterie territories remained essentially the same after the pups' arrival.

Food. — Since an aerial photograph taken in 1938 showed no burrows on Ward A, one can infer that in 1948 it had been settled for less than 10 years. The vegetation on the ward changed from its original composition of grasses to forbs (see Food Relations) between its first settlement and the time when it was first studied. Apparently the food resources of the ward were sufficient to support the resident prairiedog population throughout this period. In July of both 1948 and 1949 no marked change in the vegetation was apparent. Vervain (Verbena), mare's tail (Leptilon), scarlet mallow (Sphaeralcea), and other forbs were abundant. The vegetation in February of 1950 was remarkably different from what I had seen in the summer of the two preceding years. Most of the difference in vegetation can be attributed to the time of year, since the vegetation was dormant during the winter. The plants of the preceding summer were reduced to a few short, dried stems. Outside of the ward the tall grasses were flat on the surface of the ground, forming a mat of dead vegetation. This barren situation lasted well into June, almost a month after the pups came from the burrows. Apparently, the prairiedogs were still finding food on the ward, but their trips outside the ward onto the mat of dead grasses indicate that their feeding was supplemented by vegetation growing beyond the limits of the older sections of the ward. It is possible that the arrival of the pups intensified the necessity for feeding in the new areas, where food was available and where the vegetation was not sufficiently high or thick to obstruct the view.

As the summer months approached, the growth of fresh spring vegetation in the area of expansion preceded that on the ward proper. The added attraction of food, the foothold gained in the new area by the construction of burrows, and the lack of tall vegetation probably contributed to the expansion. When I noticed this extension of the feeding range in the spring, I predicted that the prairiedogs would move back into the old ward after the vegetation grew tall in this area and after there was more food available for them again on the old ward. The foothold in the new region was firm enough, however, to make my prediction false. They were able to control the vegetation about their new burrows sufficiently by keeping it cut. The new vegetation which grew on the older part of the ward was used by the pups. From their foothold in the region of expansion the adults began to develop that area, digging new burrows, clipping the vegetation, and making runways through the tall grass between the burrows. Some of the adults remained permanently in the area of expansion, but others continued to return to the old ward at night until the latter part of August, when all of the adults of the Red coterie moved permanently to the new area.

If it is concluded that the prostrate grass in the area of expansion during the winter and spring aided the invaders to obtain a foothold there, a similar conclusion may be drawn from the settlement around the limestone outcrop, which lacked tall vegetation, to the southwest of Ward A. The limestone outcrop, situated about 300 feet southwest of the nearest occupied burrow of Ward A, contained three old burrows tunneled beneath the exposed rocks. No use of these burrows was made in 1948 or 1949, and not in 1950 until June. From June through the rest of the summer of 1950 prairiedogs were seen on these rocks, and new burrows were dug near this outcrop. The first animals seen there were not from Ward A, but from other parts of the Shirttail Canyon town. This invasion of an area of short vegetation, an area which was not adjacent to the region of the town the animals had left, suggests that short vegetation may encourage prairiedogs to settle a new area. Of course, other factors, too, were associated with the settlement of this particular limestone outcrop. For example, some old burrows were already there, and the area was close to a town, although it was entirely undefended by the prairiedogs inhabiting the adjacent ward.

A low growth of vegetation, then, may be conducive to the expansion of a prairiedog town. Scarcity of food, particularly after a population increase, may force prairiedogs to search for new supplies outside the limits of the occupied town. In searching for the food resources prairiedogs seem to select vegetation that is neither too rank nor too tall. Their efforts to expand are aided by the winter, which allows them to gain a foothold in a new area when the vegetation has died and lies flat. They are also aided by edaphic features, such as rock outcrops, which are not suitable for the growth of tall grass. Once the prairiedogs gain a foothold, they are able to control effectively the vegetation on the new site.

Social conditions. — In addition to whatever influence the population density and the character of the vegetation may have on the settlement of new areas, the social relations of the prairiedogs must be considered. Population pressure and social repulsion are sometimes given as the cause of dispersal (Burt, 1940). In many mammals the adults apparently force their offspring from the homesite, particularly if another litter is produced in the same season (Errington, 1939; Bradt, 1939). Although the behavior exhibited in the expulsion of the young from the homesite is not known for many mammals, it is generally believed to be characterized by overt antagonism on the part of the adults.

Beyond the slight expansion of the Brown coterie territory, in which the young accompanied the adults into unsettled areas, there was no case of emigration and settlement of new areas away from the town in which the young of the year took part. All emigrants were adults or at least one-year-old animals. None of the emigrants from Ward A were yearlings (most were two years old or older). One of the individuals which moved out to the area of expansion, however, had been trapped on Ward B the preceding year when it was a pup. Consequently, it is known that yearlings do emigrate. Many of the other individuals trapped in June on the area of expansion appeared to be smaller than the two-year-old animals, and I believe that they also were yearlings.

The social factors which influence the emigration of the yearling animals may be quite different from those which influence the adults to move. With the appearance of the young on the town in spring, the yearlings which have spent the winter on their homesite may be forced to move. Rivalry among the yearling males, which increases during the spring, may result in the expulsion of all but one or two, or the coterie may be invaded by an aggressive male from a neighboring coterie, which forces out the yearling residents. Apart from these possibilities, the social relations on Ward A in 1949, when most of the individuals were one year old, indicate that there was a great deal of social instability. In early July of 1949, for example, one yearling male (No. 6) of the Blue coterie began to show considerable aggressive behavior and forced his way into the Red coterie. At the same time ♂ 4, the brother (?) of ♂ 6, which was much less aggressive but which was caught between the rivalry of ♂ 6 and the yearling ♂ 24 of the Red coterie, left the area and was not seen again. It is possible that ♂ 4 and others like him form the body of emigrants into new areas along with individuals like ♂ 6, which actively seek a new coterie. The lack of rivalry between either ♂ 6 or ♂ 4 and their presumed father, ♂ 19, suggests that the cohesive bonds between parent and offspring may prevent any display of antagonism. Some yearling males apparently leave their home coterie on their own initiative.

These one-year-old animals, most of which are males, seem to account for one type of emigrant, and the parents of the last generation of offspring form another type. The social factors causing the departure of the older adults must be quite different from those influencing the yearlings. The social relations among the adult members of a coterie are friendly, particularly after the young come out of the burrows. Similarly, the relations of the adults with the pups are friendly, except for an occasional disciplinary drubbing. Certainly, there is no antagonistic behavior which would force the adults to leave. Perhaps, then, it is the attentive behavior of the pups which motivates the departure of the adults. The pups do not leave the adults alone; they climb over them, they kiss them, they crawl under their noses when they try to feed, and they constantly interfere with all their activities. Intermittently this behavior is stopped by a drubbing, which has little lasting effect. The adults could prevent the pups from bothering them by becoming antagonistic, but this might have a serious effect on the organization of the town society. The alternative is for the adults to leave the coterie territory to the pups, where they are secure both socially and environmentally. Apparently the latter "choice" is made.

Effects of Expansion

Effect on the population. — The resulting population in the area of expansion in June of 1950 was extremely mobile, with strange prairiedogs appearing and then disappearing and with the adults of Ward A going out to the area and again returning to the ward. Even the pups from Ward A went into parts of its, but were later restricted to those sections closest to the ward. Six strange prairiedogs were captured near the limestone outcrop in early June (Table XXIII). These individuals, as well as others which were not captured, apparently came up over the forested slope from Ward D. Three of them disappeared shortly after they were captured. One of them (♂ 125) was observed on Ward D, to which he returned 15 days after his original capture. Of these six migrants, four were males, three of them apparently yearlings. One of the two females appeared to be a one-year-old; the age of the other is

TABLE XXIII
Sex, age, weight, date and location of first capture in area of expansion of two groups of prairiedogs, showing place of prior residence and areas finally occupied in August, 1950.

Number	Sex	Age in Years	Weight in Ounces	Date and Location of First Capture in Area of Expansion	Place of Prior Residence	Areas Occupied (See Fig. 9)
Group I						
6	♂	2	36	*July 3, Ed-1	Red coterie	2
8	♀	2	28	August 9, Bc-2	Red coterie	5
9	♀	2	32	July 3, ?	Red coterie	1, 2, 3, & 5
16	♀	2	35	July 3, Bd-2	Red coterie	1, 2, 3, 4, & 5
17	♀	2	30	July 6, Bc-1	Red coterie	1, 2, 3, & 5
25	♂	3 or more	34	August 7, Fc-1	Red coterie	2 & 3
64	♀	2 or more	30	August 7, Ic-1	Red coterie	1, 2, & 3
Group II						
61	♂	1	29	August 9, Bc-1	Ward B	5
77	♂	1	30	July 15, Ic-1	Ward B	1
137	♂	1	25	June 11, Bd	Ward D ?	5
140	♂	1	27	June 12, Df	Ward D ?	4
141	♀	1	21	June 14, Df-1	Ward D ?	4
125	♂	?	27	June 5, West of area	Ward D	Returned to Ward D
132	♂	1	26	June 10, Bd	Ward D ?	Left area
142	♀	?	24	June 14, Bc-1	Ward D ?	Left area

* Observed only.

unknown. Apparently, most migrants from distant wards were yearling males. Only three of the six migrants, however, remained in the area of expansion. Two were yearling males and one was a yearling female. Two other males which invaded the area of expansion had been previously captured on Ward B; one of these was known to be a yearling and the other was probably of the same age. Although these two males were caught later in the summer, it is likely that they had invaded the region much earlier. In addition to the five yearling animals from other wards which remained on the area of expansion, the adults of the Red coterie invaded the area. These animals were all two years old or older.

The composition of the population on the area of expansion ultimately consisted of prairiedogs from two sources. Five animals, mostly yearling males, came from wards not directly connected with the area. Seven other animals, two years old or older, came from Ward A, adjacent to the area of expansion. The latter group was made up entirely of the adults of the Red coterie and included five females and two males.

Effect on the environment. — Changes in the environment in the area of expansion as a result of the activities of the invaders were soon apparent. By August over 50 burrows were dug in the area, where only a few small burrows had formerly existed. Most of them were quite small, but others had large craters of freshly excavated earth, with no vegetation growing on them. Underground connections had been made between at least two burrows whose entrances were 50 feet apart. Dirt scraped onto the craters from the surface about the burrows exposed large patches of denuded earth. The vegetation about the burrows was cut off at a height of no more than two to three inches for as much as 25 feet around each burrow. In places where all the vegetation had not been clipped short, it was thinned considerably, and dead stems and blades of grass on the ground were conspicuous. Forbs characteristic of older parts of the town had not yet invaded the area in any abundance.

Effect on social relationships. — New social relationships among the prairiedogs in the area of expansion were soon established. For the most part, these social relationships were individual affairs, although new coteries rapidly began to take shape. Some members of the Red coterie mingled with younger animals from other wards, but the relations between the yearlings varied among the individuals.

The social relationships in the area of expansion became centered about five areas which had some characteristics of coterie territories. Coteries, however, were not formed up to the middle of August, and most social relationships were dependent upon individual temperaments. The Red coterie members continued their friendly relations with one another, but the frequency of their contacts was reduced by their movements and their associations with the yearling animals. Some animals were more or less restricted to their respective areas; others wandered some distance from their home territories. The five areas and the individuals associated with them will be described as they appeared August 10, 1950 (Fig. 9).

The area which was first settled (area 1; see Fig. 9) is about 150 feet from the nearest active burrows of Ward A. It consists of three large burrows, one in each of the following quadrats: Hb, Hc, and Ic. Male 77 from Ward B seemed to be restricted to this area and perhaps defended it against other males, as no other males were observed in it; however, he was on friendly relations with four of the five females (Nos. 9, 16, 17, 64) of the Red coterie which frequently visited the area but were not restricted to it.

A burrow in Fc quadrat about 75 feet to the west of area 1 is another center of activity (area 2). This burrow and the surrounding area were taken over by ♂ 6 from the Red coterie. Male 6 made frequent trips back to the Red coterie territory, even spending his nights there until August 10, after which he slept in his new burrow. His frequent trips back to the Red territory were continued during the day. When returning to the Red territory, he avoided the area surrounding ♂ 77 by going through areas of tall grass without burrows. All of the female's that used area 1 burrows visited area 2. This area decidedly belonged to ♂ 6, but upon occasion ♂ 25 came over, usually when ♂ 6 was back in the Red territory.

The third center (area 3) of activity is within Ed and Dd quadrats, lies about 65 feet to the west of Fc-1, and is connected by a well-worn runway to Fc-1. The burrows in Ed-1 and Dd-1 are connected underground. This area was defended against all males in the area of expansion by ♂ 25 of the Red coterie. Male 25 was observed in territorial disputes with ♂ 61 and ♂ 140. Again, the four females from the Red coterie utilized this area.

The fourth center of activity (area 4) is larger than the preceding three and contains most of the limestone outcrop and several quadrats to the east of it, including Bd, Ce, Df, and Ef. This area was occupied by ♂ 140 and ♀ 141. Female 141 remained primarily about quadrats Df and Ef, but male 140 transversed the entire area of activity. Male 140 was an aggressive yearling who frequently tried to invade other centers of activity in the area of expansion as well as coterie territories in Ward A; however, he was unsuccessful and began to defend his own territory. There was only one transient female in his area. This was ♀ 16 from the Red coterie, whom ♂ 140 seemed to tolerate. No contacts were observed between ♀ 16 and ♀ 141.

The fifth area (area 5) is the farthest away from Ward A. It is situated about quadrats Aa and Bc, which included the southern part of the limestone outcrop. Two males (No. 61 and 137), which were on friendly terms with each other, were restricted to it. Female 8 from the Red coterie seemed to limit her activities to this area, although she undoubtedly could have visited the other areas along with the other Red coterie females. All of the Red coterie females except ♀ 64 were observed in this area associating with the two resident males.

In the area of expansion coteries were thus beginning to form, although they still were not discrete units like those in the older parts of the town. Males from both groups of migrants staked out territorial claims, which they defended against other males, but the females were at liberty to move indiscriminately among these territories, Some females, such as No. 8, 64, and 141, were less mobile and seemed to spend most of the time in a single area. Other females, such as Nos. 9, 16, and 17, wandered all over the area of expansion. Female 16 continued to make frequent trips back to the Red coterie. The social relations among the animals of the Red coterie were essentially the same as they had been, except that the females became friendly with the young male migrants. There had not yet been any display of territorial defense by the females, such as would occur in a well-formed coterie. The five areas occupied and defended by males appear to be incipient coterie territories. The animals in these territories will unite into coteries only after all movement between the territories ceases and the social relations within each territory become more intimate and exclusive.

Section Summary

The expansion of Ward A affords an excellent opportunity to study the possible causes of emigration and its subsequent effect upon the environment and upon prairiedog social relations. Although no definite conclusions can be drawn, some of the factors that affect the expansion of a prairiedog town have been ascertained. First, there are two principal types of migrants: one type consists of yearling animals, mostly males; the other type, of animals two years old or older of both sexes, although females are the more abundant. Second, behavior of the two types of migrants appears to be different. The young animals move long distances, cross uninhabited regions, attempt to colonize any suitable habitat, and seldom return to the home coterie. They may linger about the periphery of the town and may attempt to invade stable coteries from time to time. The old animals move short distances from their home territory, establish themselves with burrows as they move farther away from the old town, and frequently return to the home territory until they are well established in the expanded area. Third, the colonization of a new area by both types of migrants appears to be facilitated on areas where the vegetation is neither tall nor dense. Fourth, in the areas of expansion new coteries begin to form by August, with a restriction of the males to defended territories, whereas the females wander freely among the male-held territories. Fifth, expansion occurs in the early part of the summer. Sixth, the young animals born in the spring do not emigrate and are kept out of the areas of expansion adjacent to the town by the adults.

The factors which cause the young prairiedogs to emigrate may be quite distinct from those which cause the emigration of old animals. When the prairiedogs become one year old, they appear to be restless and antagonistic, as in 1949, when the population on Ward A was composed mainly of yearlings. Antagonism, whether toward parents, siblings, or other coterie members of the same age, is seldom exhibited by the yearling males. Rather, they tend to invade adjacent territories where they may successfully vanquish the defending male and drive out or subjugate other yearling males. These yearling males, expelled from their coterie territory by an invader, or leaving in search of a new coterie, apparently constitute one type of migrant. The social unrest which may cause the yearling animals to emigrate is not present in the coteries which are abandoned by the old prairiedogs. The old animals, which have just raised a litter of young, may leave the coterie in an effort to escape the demands for attention made by the pups, or they may leave the coterie territory in favor of areas where they have found more abundant food. It is possible that the adults respond more readily to " population pressure" than the young and consequently leave. Whatever causes the older animals to emigrate, it cannot be antagonism or social unrest, which may cause the dispersal of yearlings.

DISCUSSION AND CONCLUSIONS

Prairiedog towns are densely settled areas including thousands of individuals, with often as many as 35 prairiedogs per acre. These large concentrations of animals are divided into small social groups of 2 to 40 individuals. Each group usually contains a male, several females, and their young. Each of these social groups or coteries, as I have called them here, occupies a particular territory, which is defended by all the members of the group. The distribution of the inhabitants in a town is uninterrupted by the territorial boundaries between coteries. Only the antagonism exhibited between members of adjacent coteries indicates that a boundary exists. This antagonism is most often displayed by a ritualistic dispute at the border of two territories, where the combatants take turns in rushing at each other with their tails raised and spread and their teeth chattering. In contrast, the members within a coterie exhibit mutual care in grooming, constructing burrows, and defending their territory against outsiders. Disputes within a coterie are unusual, except among the young animals engaged in play fights. A social hierarchy is not perceptible unless there are two adult males, one of which may dominate the other. One male in the coterie is more active than other members in guarding the territory and in identifying all individuals that may be present.

The unique social organization of the prairiedogs among North American rodents raises the question, why do prairiedogs have this particular type of organization? One answer to this query is that their social organization benefits the animals sufficiently to increase their chances of survival and reproduction. The social adaptations of prairiedogs apparently were favored by selection. Although a group of animals organized into a society may be selected as a unit, the final mechanisms of transmission of the society from one generation to the next reside in the individual. To a certain extent these mechanisms are conveyed through the germ plasm which unfolds into innate patterns of behavior. It is possible, however, that some of the mechanisms involved in the transmission of the society from generation to generation are those acquired through learning. Thus, a prairiedog town may have a cultural continuity. It is the purpose of this discussion to suggest (1) the selective advantages prairiedogs derive from their social organization and (2) the part early development of the individual plays in the maintenance of the society.

The selective advantages prairiedogs derive from their social structure are (1) the limited control over the environment through the combined activities of the inhabitants and (2) the prevention of overcrowding. The first of these advantages brings about an increase in the population density by creating a favorable environment for survival. Population increases are limited, however, by a social organization which serves to distribute the population evenly and to induce migration. In contrast to an unorganized aggregation which has no control over the environment or the population, the organized towns of prairiedogs control both to a considerable extent.

Certain beneficial modifications of the environment of prairiedog towns result from local populations with high densities. A few scattered individuals could not bring about these modifications. It has been pointed out that the population density of a town averages about nine animals per acre and varies from four to 15 individuals per acre. One local area (coterie territory) reached a temporary density of about 35 individuals per acre. The activities of individuals in such large concentrations are almost certain to bring a change in their environment.

The most conspicuous environmental controls the prairiedogs have brought about by their concentrated populations are the burrows, the modification of the vegetation, and the defense against predators. The destruction of much of the original grass cover by the animals' feeding exposes the soil to invasion by a variety of rapidly growing forbs. These forbs resist the feeding of the prairiedogs to some extent and provide them with vital foods and moisture in the form of seeds, fruits, and succulent leaves. The subsoils exposed about the entrances to the burrows are open to the invasion of other types of forbs, which provide food for the animals near a safe refuge. The burrows themselves, averaging more than 50 per acre, modify the environment to such an extent that prairiedogs seldom need go far to seek refuge from a predator. In addition to the shelter offered by the burrows, a prairiedog society is protected against predation through the combined watchfulness of its members and their ability to warn one another of the approach of danger. Not only does this warning system relieve each individual of the full burden of caution and permit it to carry out its other activities with little interruption, but it also multiplies the probability of detecting the approach of a potentially dangerous enemy.

The advantages which prairiedogs derive from living together might easily be lost without some regulating mechanism to prevent their population density from becoming too great. In the absence of any such regulating mechanism, the densely populated areas within a town might be stripped of all the available food, and foraging trips away from the burrows might expose the prairiedogs to heavy losses through predation. Parasitic epidemics might destroy the entire population, or fighting between individuals might create disturbances that would prevent the animals from carrying out their normal activities. Such overcrowding, however, is avoided by properties inherent in the social organization of the prairiedogs. This population-regulating mechanism is a self-contained system that is not dependent on such controls as predators and parasites (Elton, 1942).

The sociality of prairiedogs operates as a population-regulating mechanism in three important ways: (1) the defense of territories by the coteries ensures a somewhat equal distribution of the population throughout the town, (2) migration, dispersal, and mortality are affected by the social behavior of the prairiedogs, and (3) the stable social organization within the coteries provides a suitable social environment for successful mating and rearing of the young.

The organization of the population of a prairiedog town into discrete units prevents overcrowding on any particular area. Although the population density on Ward A fluctuated during 1948-50, the number of adult prairiedogs in each coterie territory remained more or less equal within the ward. This distribution of prairiedogs throughout the area of each ward prevents overgrazing in any one locality. Unlike the dense population of the warrens of the European rabbit (Oryctolagus cuniculus), where practically all of the vegetation is depleted and the inhabitants are required to forage in the areas surrounding the warrens (Southern, 1940), the even distribution of prairiedogs in the town is not likely to deplete the supply of food near their burrows; thus prairiedogs can feed near the refuge of their burrows. Consequently, the social behavior which divides the prairiedog population into local groups tends to keep the density of the groups in harmony with the local food supply. Starvation or malnutrition is prevented, and exposure to predation is reduced. At the same time, the prairiedog population is large enough to keep the area free from dense vegetation which might conceal the presence of a predator.

In addition to ensuring an adequate food supply, the organization of the population into coteries provides each inhabitant with numerous burrows to which it can retreat should a predator approach. An individual seldom has to run more than few yards to the nearest burrow in case of danger. Furthermore, an individual, hard pressed by a predator, does not have to run to a particular burrow, but may run into any burrow close at hand, since all the burrows within the coterie territory are used by all members of the coterie. In contrast to the readiness with which an individual darts into any burrow on its coterie territory, an individual outside its territory runs from burrow to burrow and must be very hard pressed before it will enter an unfamiliar one. When a stranger is forced down a burrow outside of its territory, it soon reappears and makes an effort to return to its own territory.

The regulation of the population by means of social behavior is also effected through migration, dispersal, and mortality. It has already been pointed out that emigration of certain individuals over one year old occurs. One category of emigrants consists of members of the one-year age class, predominantly males which are either forced from their natal territories by the hostility of invading males or leave voluntarily. It is likely that such voluntary emigration is often socially determined, since a young emigrant male presumably attempts to find a coterie which he can dominate. A young male which remains in his natal territory usually becomes subdominant to another male. More often, the young males move out when exposed to aggression by other males. The other category of emigrants is composed of individuals two years old or older, mostly females, which have raised their offspring to the age when they are independent of their parents. The social pressures which motivate female emigrants of this type are not well understood, particularly if one does not wish to attribute any foresight to the animals. One is tempted to say that they leave the resources of the old territory to the young in order to prevent a shortage of food and burrows and to prevent any possible outbreaks of hostility among the coterie members. Such speculation is, of course, unwarranted, and if social factors are at all responsible for their departure, one such factor may be the escape from the persistent attention given to them by their offspring. It is also possible that these emigrants are attracted to new areas by the more bountiful supply of food (see Expansion of the Town).

The extent to which social behavior influences emigration is difficult to ascertain, but the effect of emigration on the population is quite evident. First, it reduces the density within the town. The Red coterie territory, for example, had a greater density in May, 1950, than any other coterie territory on Ward A. The emigration of the adults from the Red territory in June and July of that year reduced this density from 39 to 32 individuals on the .92 acre of land they inhabited.

Second, emigration may expand the area occupied by the population. Ward A, for example, increased from 5.2 acres to 7.3 acres as a result of the 1950 summer migration.

Third, it disperses the population, which utilizes new resources and creates new breeding assemblages. The expansion of Ward A into the uninhabited adjacent area was undertaken by individuals from many parts of the town. New coteries formed, which were composed of the older inhabitants of Ward A and young adult males from other wards in the town. These new coteries aid in spacing the population, since the offspring of those adults which migrated to this adjacent area from Ward A were kept out of the new area. Further, the recombination of individuals in the newly established coteries provides different mates and ensures genetic variability in the next generation.

Fourth, emigration affects the population through mortality. Prairie-dogs away from their burrows are especially vulnerable to attack by predators. Since migrants often travel over areas which lack burrows, many are probably killed during their wanderings. Mortality must be particularly high among the young males, which usually make the longest migrations. The mortality of these males is apparent in the reversal of the sex ratio between the time when the young come out of their burrows and the time at which they breed a year and a half later. The sex ratio of the young on Ward A in 1950, for example, was 1.5 males to 1 female. Among the adults, the sex ratio in 1950 was 0.7 male to 1 female (Table XII). Some of this change in the sex ratio may be attributed to successful emigrations of males to other areas, such as occurred in the area of expansion on Ward A in 1950. The disappearance of those males which left Ward A, however, suggests that they died. One male, No. 10, for example, disappeared from the Brown coterie in March, 1950, while breeding was in process. This male, which was an adult when first captured in 1948, and which remained on Ward A until he finally disappeared, was observed for the last time in an uninhabited area adjacent to the ward, after being chased there by ♂ 37. Mortality caused by enforced evacuation from the town may be particularly high if such rivalry is intense during the breeding season.

The third way in which social behavior operates as a regulating mechanism is by its effect upon the amount of reproduction. The social behavior of prairiedogs favors an increase in the number of young produced and raised. During the breeding season all members of the coterie are acquainted with one another, and the social relations are well established. A female which comes into estrus is assured of a mate at the proper time for conception. Barren females within a stable coterie appear to be unusual. The only barren female in 1950 on Ward A was No. 1, which was a member of an unstable coterie. Calhoun (1949a) has clearly demonstrated that the reproductive potential of house rats (Rattus norvegicus) is considerably reduced among females living under adverse social conditions. The polygynous pattern of mating among prairiedogs is a further insurance against barrenness in potentially productive females. Usually each coterie contains only one adult male, which eliminates competition between males at this time. Fighting between males may interrupt breeding behavior, as J. W. Scott (1950) has pointed out for the prairie sharptail grouse (Pedioecetes phasianellus). Such disturbances may reduce the amount of reproduction. As mentioned previously, males of different coteries may fight, and occasionally one may succeed in temporarily usurping the territory and females of another. The effect of such antagonism on the success of mating is not known, although it may be detrimental should it occur at the height of the breeding season. In the Brown coterie, which was temporarily taken over by the adult male of the Red coterie, the five resident females produced only 14 young in contrast to the five females of the Red coterie which produced 32 young. This difference in the fertility of the two coteries cannot be attributed solely to the rivalry between males, although that may have been a contributing factor.

During the development of the young, social behavior is of further importance for their successful rearing. While the young are still in the nests, most mothers defend the natal burrows against all other members of the coterie. In this way the helpless offspring are assured a quiet social environment during their early development. It is interesting that the five females of the Red coterie, which defended their nests much more vigorously than did the five females of the Brown coterie, raised over twice as many young. After the young emerge from the burrows, the defense of nest burrows abruptly terminates, and the young are permitted to wander throughout the entire coterie territory. They are given friendly and affectionate treatment by all the adult females and males of the coterie and play with one another indiscriminately. They are protected against strange individuals by the territorial defense of the adults. Such a friendly social environment for the young gives them a safe place to grow and mature, quite unlike the deleterious social conditioning which house rats may receive (Calhoun, 1949b). Nor are the young forced out of their natal territories by hostile parents after they are weaned, as are young muskrats (Errington, 1939). Instead, the adults often abandon their territories to the young when they no longer depend upon the adults.

The importance of the favorable social environment for the young prairiedogs is evident in their extremely low mortality during their first summer of life. On Ward A only one pup out of 58 succumbed after the young first emerged from the burrows. The death of this one pup was due in part to illness. Such low mortality among the young is rare in most species of rodents. The mortality rate of prairiedogs does increase after their first summer, but the reason for this is not known.

Not only is the social organization important in preserving the young, but through the social conditioning which they receive the organization is perpetuated. The social milieu into which a young prairiedog enters when he first emerges from his burrow is far more complex than his previous associations, which were limited to mother and siblings. Within the first few hours or, at most, days, he may meet his father, other males, other females, and numerous young animals no older than himself. The nature of these contacts is important in his young life, for the conditioning he receives from them may well determine his later social relationships. The fact that all adults treat him as his mother does (grooming him, for example) tends to make him respond to them as he does to her. This is indicated in his readiness to accept foster mothers and in his attempts to suckle males. The dissolution of the nest territories when the young first emerge enhances his chances of meeting many strange but friendly coterie residents. It is his period of socialization (Scott and Marston, 1950), and the opportunities for social contacts are abundant. Within his first week or two he may wander into an adjacent coterie territory without resistance from the resident animals.

The first few weeks, then, expose the young prairiedog to many new and amicable social contacts. He plays with his siblings and other young prairiedogs. He nurses or tries to nurse all the adults of both sexes. The adults receive his attempts passively, or they begin to groom him, push him gently away, and often lay him down and run their teeth through the fur along his belly. There is no kicking, biting, or drubbing the weanling. His demand for this affectionate treatment increases, and he follows the adults around, climbs over them, crawls under their chins, does everything he can to invite grooming. On rare occasions he is so demanding that he may be temporarily repulsed by the adult. Sometimes, when he fails to gain the attention of the adults, he may jump at them in play and is occasionally rewarded by reciprocal play from them.

As the young prairiedog matures, he wanders farther and begins to meet with hostilities when he invades adjacent territories. At first, the aggression displayed by the residents of the invaded territory is mild, but gradually it becomes severe. Soon he recognizes the territorial boundaries and learns that all prairiedogs do not treat him alike. He discriminates between coterie members and strangers; the identification kiss, which apparently is innate, serves this function. If his kiss is not returned by another animal in his territory, he treats it suspiciously, barks at it, runs up to smell it, and then dashes away. This behavior later develops into the tail-spreading ritual. When he is in a strange territory, he acts cautiously and runs to his own territory at the approach of the resident animals.

Soon after he comes from the burrow he begins to utter territorial calls, either in response to others or spontaneously. When he utters them outside his territory, he is immediately attacked. Later, he limits them to familiar areas where they become associated with his well-being. He hears the call given by other coterie members only when all is safe, and he responds when he also is secure. After a threat by trap, stranger, or eagle, he hastens to communicate his feeling of security to other members. These responses become more specific as he learns the objects that threaten him. In a similar manner he barks at all strange objects, such as a magpie or even a robin, but soon he learns to limit his barks to objects which might be a real danger.

By the end of the summer, the young prairiedog has become adept in exhibiting the behavior which is essential to the organization of the town. His play is less frequent and now resembles real fighting. His associations with adults are fewer because of their departure from the home territory. When he does encounter them, he may groom them as often as he himself is groomed. He keeps within his territorial limits or invades only uninhabited areas. He guards his territory against invaders, particularly those of his own age. Adult invaders stimulate his barks, which attract coterie members, and the invader is driven away. He has matured now except for his sexual behavior.

The behavior of the yearling during the breeding season has not been thoroughly studied. If adults still reside in the coterie territory, a yearling male may show interest in the females, but this interest is probably checked by the aggressive actions of older males. He may attempt to leave his territory at this time, which possibly explains the high mortality of yearling males between September and June. His sisters, probably not in heat at this time, do not engage in sexual activities. If the yearling male remains in the coterie until summer, his disputes with other yearling coterie members may increase. He shows no antagonism to the adults or to the young pups now coming from the burrows. In June and July, as his fights with other yearlings become more severe, he grows restless and invades other territories, constantly testing the combative qualities of strange males. If he finds a weak neighbor, he may contest with him for the territory. Should he succeed in establishing himself in a new coterie, he dominates the other males, or they leave and try to gain new territories for themselves. If he is less aggressive, he may be forced out of his territory by an invader and may either search for a new one or go to some uninhabited area near the town.

In a newly settled area other prairiedogs may be attracted to his site. Yearling females which have been crowded out of the old territory by the new crop of pups, or adult females departing from their young, may come to live with him. Other yearling males which have left their original territory may join him. Into the new territory prairiedogs bring the social order practiced in their youth. Strangers are repelled, and acquaintances are recognized and cared for. The male is sexually mature at the next breeding season and mates with the adult females of his coterie. The social behavior and organization adaptive for preceding generations are again duplicated in preparation for the next generation.

SUMMARY

A large town of black-tailed prairiedogs (Cynomys ludovicianus) which is located in Shirttail Canyon, Wind Cave National Park, South Dakota, was studied during 1948, 1949, and 1950. This town is divided by topographical and/or vegetational features into semi-isolated units, here called wards. All of the inhabitants of Ward A, covering 5.2 to 7.3 acres, were live-trapped and marked. The behavior of the marked prairiedogs in their relation to the physical, biotic, and social environment was observed.

The environment of a prairiedog town is characterized by numerous burrows and by a depletion of the original grass cover and its replacement in part by forbs. On 9.4 acres of the Shirttail Canyon town, the density of the prairiedog burrows was 57 per acre in 1948. Most of the original cover of grass in Ward A had been replaced by a large variety of forbs. In the middle of the town fewer species and fewer individual plants grow than at the periphery.

Prairiedogs spend an average of 57 per cent of their active day feeding. Various species of plants are used for food, forbs being among the most important.

Prairiedogs are strictly diurnal, but show no other daily periodicity. They are less active during the winter than during the summer.

Mating occurs during February and March. Young prairiedogs appear above ground in the middle of May. By the end of the summer the young weigh nearly two-thirds as much as the adults. Adult size is reached near the middle of their second summer. Mature males average more in weight than mature females, except when the females are pregnant. The prairiedogs on Ward A did not reproduce until they were almost two years old.

Mortality is low among the young during their first summer of life. It increases, however, after their first summer, particularly among the males. This is shown by the fact that the ratio of males to females among the young during their first summer was 1.5:: 1.0, whereas the ratio for the adults was 0.8 : 1.0 for the period of study.

Predation was only a minor cause of mortality among prairiedogs during the period when Ward A was under observation.

The number of prairiedogs on Ward A fluctuated throughout the three-year period of study from 4 to 15 individuals per acre with an average density of 8.9 individuals per acre.

The individuals within each ward are organized into discrete social units, here called coteries. The mean number of all individuals per coterie during the period of study was 8.5 (2 to 35). The mean number per age class and sex within each coterie was 1.65 adult males, 2.45 adult females, 3.57 immature males, and 2.36 immature females. The territory occupied by the coterie is defended against nonmembers. The average size of the coterie territories in Ward A was 0.70 acre, which is also the mean home-range area for each coterie member. Movements of a prairiedog are unrestricted within its coterie territory. The mean distance traveled per day by seven individuals whose movements were recorded was 5,524 (3,200 to 14,112) feet.

The individuals within a coterie are socially integrated. Group coordination and control is achieved through reactions to tactile, olfactory, visual, and vocal stimuli. Responses to tactile stimuli include kissing, grooming, playing, and fighting. Responses to secretions of the anal glands were noted. Vocal communications include warning barks, defense barks, territorial calls, fighting snarls, fear screams, and tooth chattering.

Prairiedogs within the coterie co-operate with one another, but they exhibit little division of labor. Direct competition for food and shelter is uncommon within a coterie. All the members occupy a nearly equal social position, and there is no distinct social hierarchy.

Numerous amicable interactions among all the members of each coterie result in social cohesiveness. Cohesion within the coterie is interrupted by antagonistic behavior during the period of reproduction, when nesting territories are defended temporarily be each breeding female.

Social relations between the members of neighboring coteries are antagonistic in the defense of their respective coterie territories.

The town population is integrated by the vocal communications of the inhabitants and by the occasional interchange of members of coteries.

The expansion of prairiedog towns into adjacent uninhabited areas occurs in the early part of the summer by the formation of satellite colonies composed of individuals originating from various coteries and wards. New coteries are formed in these colonies by males who preempt certain territories before the females become restricted in their movements to a particular coterie. Young prairiedogs of the year do not take part in the formation of new colonies.

Expansion of the town and the formation of colonies near the old town prevent the depletion of the food resources within the old town, which would result from overcrowding.

The social behavior of prairiedogs, including the defense of coterie territories, is a mechanism which regulates their local population density.

Prairiedogs are adapted to their environment because of their ability to control such features as the height of the vegetation, the relative amounts of grasses and forbs, and the number of their burrows. Their exposure to predation is reduced by their social habits and by their modification of the habitat. These results can only be accomplished through the combined activity of a group of these animals. Social behavior and social organization are consequently very important factors in the adaptation of prairiedogs to their environment.

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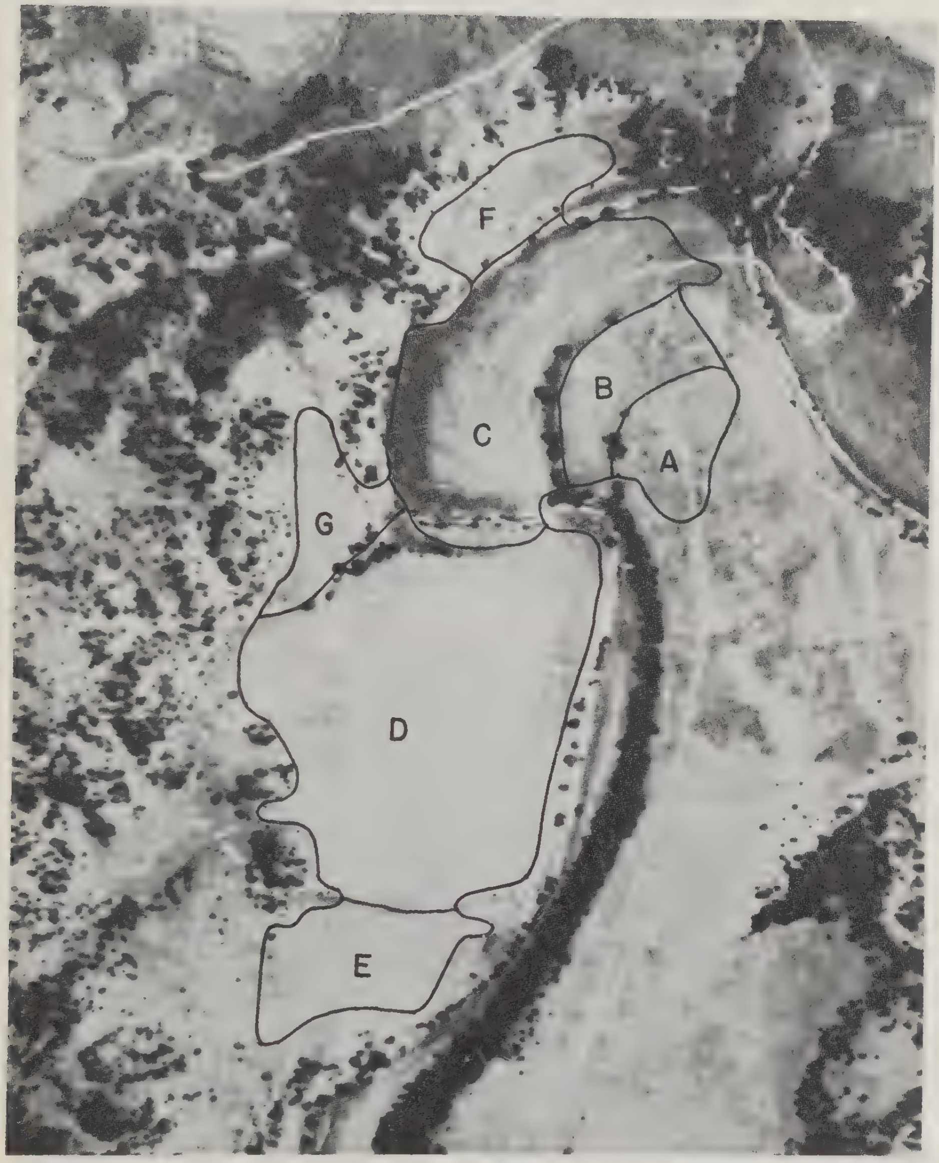
PLATE I



Aerial photograph of Shirttail Canyon taken in 1938. Letters indicate wards of the prairiedog town in 1950. Ward A was the study area.

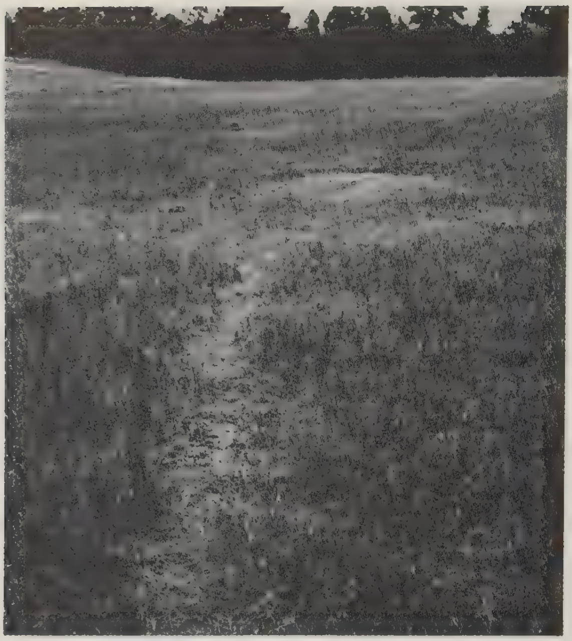


FIG. 1. Prairiedog runway through tall grass between burrows in a recently settled area. The runway leads directly to a burrow.

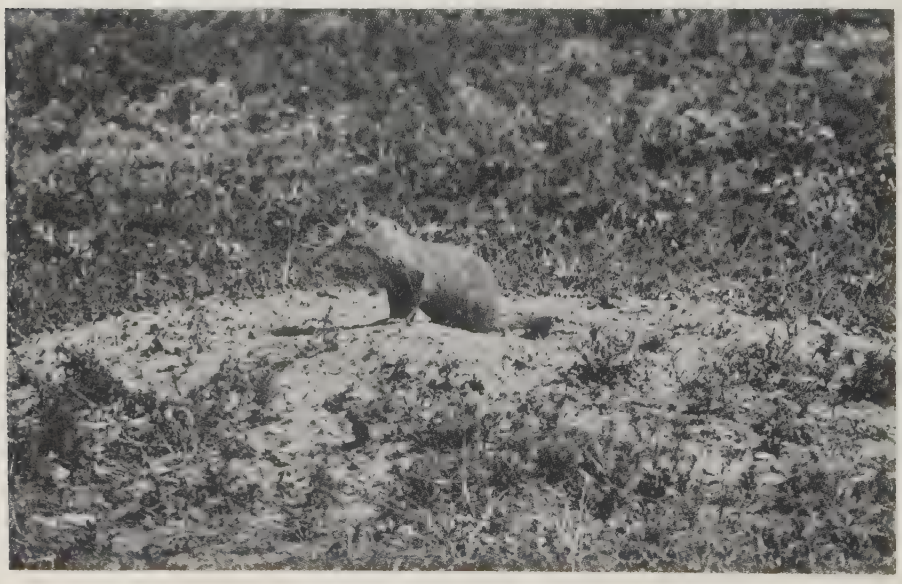


FIG. 2. Adult female carrying nesting material into a burrow.

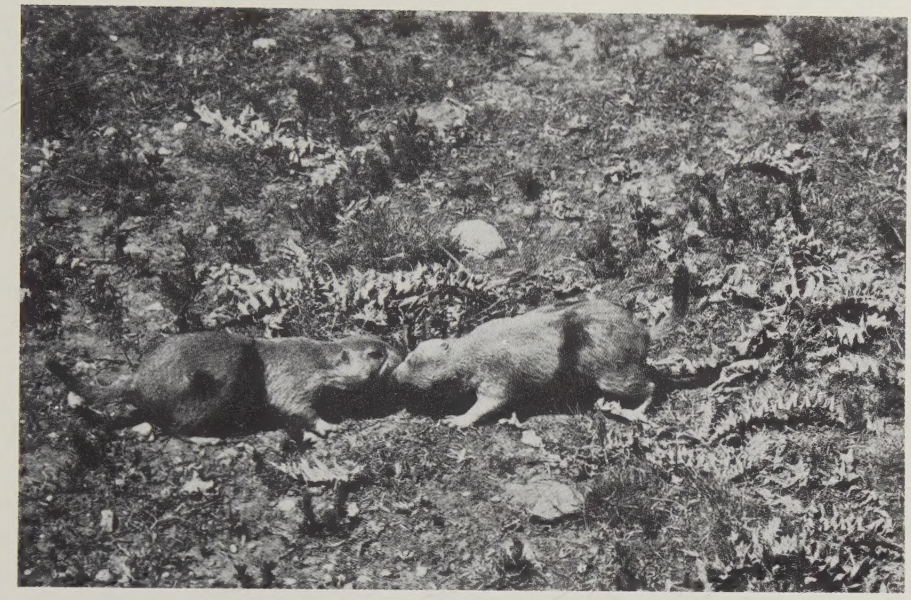


FIG. 1. Identification kiss between young prairiedogs of the same coterie.

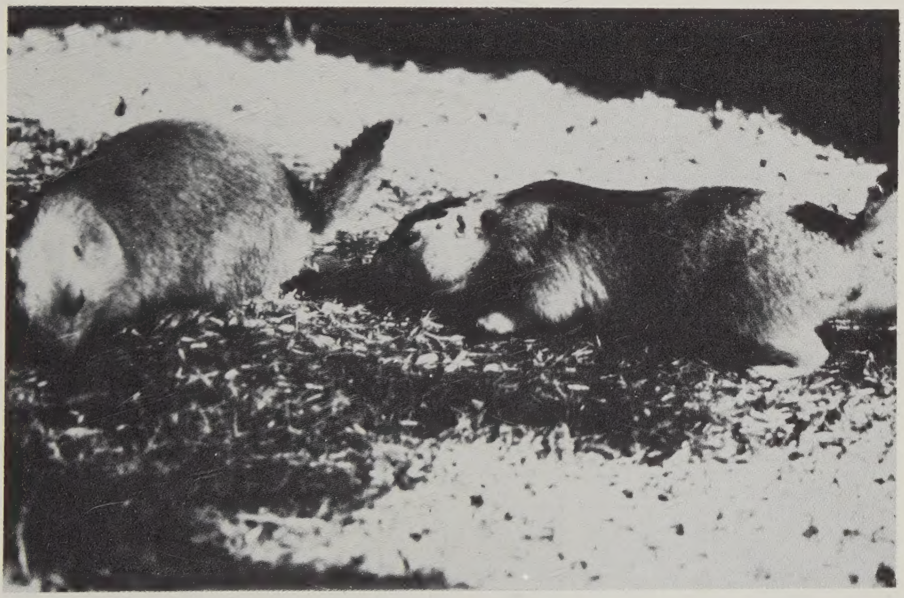


FIG. 2. Tail-raising dispute between two female prairiedogs of different coteries. The individual at the right of the figure is approaching to smell the anal region of the other, whose tail is raised and spread.

PLATE IV

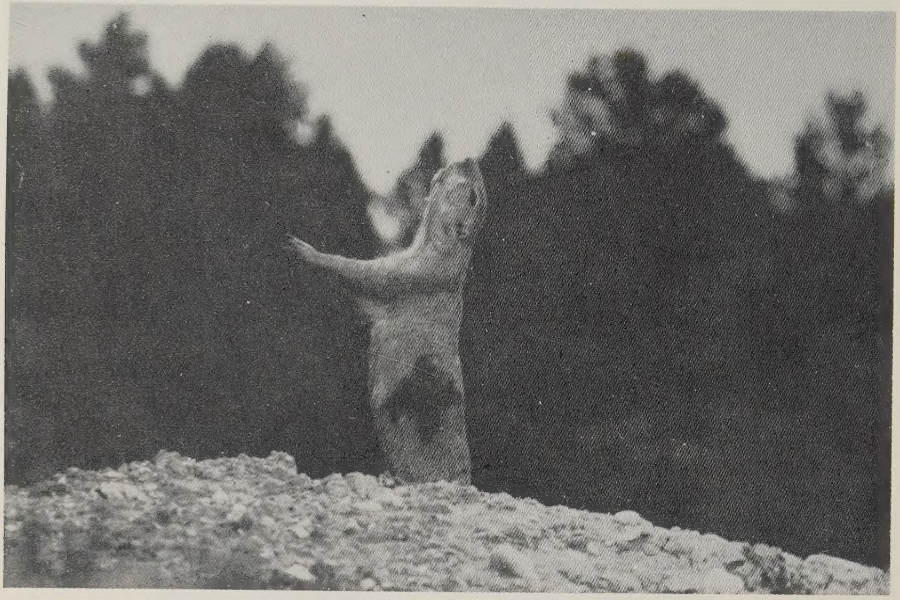


FIG. 1. Territorial call given by an adult female at the entrance of her burrow.

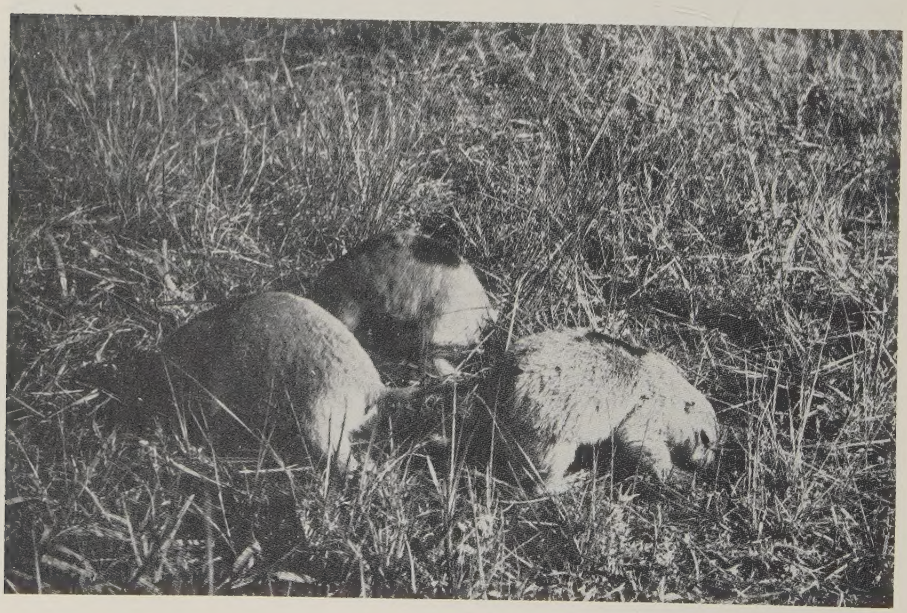


FIG. 2. Three prairiedogs co-operating in the construction of a burrow crater.

3 9001 01783 5110